The Experimental Study of the Chemotactic Basis of Host Specificity in Phytophagous Insects

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Introduction

The high degree of host specificity of many phytophagous insects is a commonplace, yet remarkable phenomenon. Nevertheless it has been relatively neglected as a field for experimental study.

The first beginning was made about 50 years ago when Grevillius (1905) found that the larvae of the browntail moth *Euproctis chrysorrhoea* (L.) which feeds on the chick weed, *Stellaria,* could be induced to feed on other plants by smearing the leaves with a paste containing tannin which is a constituent of chick weed. It is unlikely that this work was highly critical with respect to the chemical purity of the test preparations, yet the basic principle inherent in all experimentation in this field was employed. That is to say, a relatively isolated chemical constituent of the host plant together with some ingestible substrate other than the host plant tissue was offered to the insects. Obviously, the induction of feeding indicated that the test material contains some substance that stimulates the appetite of the insect.

Five years later, Verschaffelt (1910) made the elegant observation that the distribution of the mustard oil glucosides among plants coincides with the range of acceptable host plants for the larvae of the butterflies, *Pieris rapae* (L.) and *P. brassicae* (L.). He naturally inferred that the mustard oil glucosides or their fission products stimulate feeding in these insects and he performed some simple but significant experiments that confirmed this hypothesis. His experimental technique, however, was the same as that of Grevillius and was inadequate to permit a complete analysis of the various factors involved.

This work of Verschaffelt was justly considered a classical contribution to our knowledge and yet it failed to stimulate further significant work for many years. Ultimately, a renewal of interest was stimulated in France by the ravages of the Colorado potato beetle. This insect, as is well known, is oligophagous, and is even more discriminating than the cabbage butterfly in that it will eat only some species in the genus *Solanum* and a few other plants. The French workers, Raucourt and Trouvelot (1936) and their associates believed that a knowledge of the physiological basis for host plant selection would be of value in arriving at a control for this pest and set out to isolate the host constituent that induces feeding. Although they introduced an ingenious technique for testing the palatability of their extracts, they did not isolate the substance they sought in a highly purified form. This was finally accomplished by Chauvin (1945) (1952) who described some of the chemical properties of the feeding stimulant and showed that it gives reactions characteristic of flavone glucosides. Its precise identity however, remains unknown. Chauvin also refined his predecessors' methods for testing the palatability of plant extracts.

More recently the explanation of the feeding behaviour of the Colorado potato beetle has been complicated by the findings of Hesse and Meier (1950) who found that acetaldehyde induces both adults and larvae to feed on gelatin. The properties of acetaldehyde seem to preclude the possibility that it is identical

with the substance isolated by Chauvin.   As we shall see later there is no necessary contradiction between these findings.

In America, a significant contribution was made by Professor Dethier (1941) who studied the influence of certain essential oils on the feeding of *Papilio* spp. and related these to the probable evolution of species in this genus of insects. Since then he has published illuminating reviews and discussions on the biological significance of host specificity (Dethier, 1953, 1954).

In England, at the end of the war, I had the opportunity to investigate the chemotactic basis of host specificity in the diamondback moth, *Plutella maculipennis* (Thorsteinson, 1953).   This insect has the same host range as the *Pieris* spp. studied by Verschaffelt (1910) and the mustard oil glucosides were again found to be the significant feeding stimulants.   By the use of a suitable technique, it was possible to investigate the role of enzymes that hydrolize the glucosides as well as the enzymatic fission products and to pave the way for a study of the nutrition of this insect.   Since then, at the University of Manitoba, I have confirmed some of the work of Chauvin with the preliminary object of simplifying his laborious method of isolating the feeding stimulant in potato leaves. Another project is now also underway which concerns the host relations of the sweetclover weevil, *Sitona cylindricollis* (Fahr.).

The time is now opportune to outline and evaluate what seem to be the most effective experimental techniques in order to encourage research in the fertile and little studied field of the physiology of host selection.   This discussion is limited to insects with chewing mouth parts.   Methods applicable to plant sucking insects are discussed in a recent paper by Maltais (1952).

Methods of Measuring Feeding Responses to Extracts

The simplest method of testing extracts of host plants is that used by Grevillius (1905), Verschaffelt (1910) and Dethier (1941).   It consists of smearing or painting the leaves of plant species not normally eaten by the insect with leaf extracts or other test preparations.   The limitations of this ruse is that negative responses are difficult to interpret and cannot easily be made quantitative as to dosage.   For studying feeding inhibitors, Kuhn and Gauhe (1947) infiltrated the leaves of the host plant in test solutions under reduced pressure.

With some insects it may be impossible to find an experimental non-host plant that contains no unpalatable substances that would interfere with feeding responses.   In consequence, it is desirable to devise a neutral substrate or artificial leaf.   The first attempts of this kind utilized filter paper.   The number of holes eaten in treated paper provided an estimate of the palatability of test substances. This served its purpose well enough in studies on wireworms (Thorpe, *et al.*, 1947), *Papilio* larvae (Dethier, 1941) and grasshoppers (Chauvin, 1951) but paper is too tough and fibrous for many smaller and weaker insects.   The use of slices of elder pith to be described later is much superior.   I have tested a number of possible substitutes such as collodion and albumen but none are satisfactory as they expand or contract violently with changes in moisture.

In the study of the diamondback moth (Thorsteinson, 1953) the test substances were incorporated in an agar gel along with dehydrated powdered leaves or other nutrients.   The amount of feeding was estimated by counting the number of frass pellets produced by the larvae.   This method should work well with caterpillars and chewing insects that can feed on a flat surface and produce discrete frass pellets that are reasonably uniform in size.   Weighing the frass, if practicable, is of course better than counting them.   Advantages of this technique are that the texture and moisture content of leaves can be closely approxi-

mated and the combination of various mixtures of test substances can be prepared in sufficiently accurate proportions with facility. This method is particularly applicable if the objective is to develop a synthetic diet for nutritional studies. It is less useful, however, if it is desired to simulate the form of a leaf as when an insect feeds only from the edges. It is not suitable for insects such as the Colorado potato beetle that produce semi-liquid faeces.

The most useful technique yet developed is that introduced by Raucourt and Trouvelot (1936) and later improved by Chauvin (1945). This involves the use of elder pith as a mechanical support for the extracts. The pith is cut into discs of the thickness of the host leaves on a microtome. The discs are then cut to a uniform circular area with a sharp cork borer or similar die made from a steel tube. These discs are pressed flat and dry between sheets of blotting paper and stored in a dry container. In experiments the discs are mounted on waxed paper in dishes.

Chauvin's technique may be modified slightly to advantage in some respects. He mounted the discs on waxed filter paper in glass dishes using a hot plate to seal the pith to the wax. I have found it preferable to mount the discs on the filter paper immediately after it is treated with molten wax from a hot water bath when the wax is congealing as there is less danger of overheating and saturating the discs with wax. Chauvin used a micropipette to treat the mounted discs with known volumes of the test solutions. Since the discs are of a standard thickness and area I have considered it sufficient and expedient in preliminary experiments simply to immerse the discs in the test solutions, drain off excess solution and dry the disc before mounting on the wax paper. The discs are then moistened with water to render them more succulent. A convenient way to do this is by the use of an atomizer connected with a source of pressure such as a carbon dioxide tank.

This method has worked well with the Colorado potato beetle but a modification was necessary for the sweetclover weevil because it will not chew a flat surface but almost invariably eats notches from the sides of leaves. This difficulty was overcome by clipping the pith discs in the split end of a short length of applicator stick. This wooden stem was then fastened with wax to filter paper lining the floor of a small plastic dish. This enables the weevils to straddle the raised edges of the discs during feeding in their characteristic way.

After an adequate feeding period, the insects are removed. The remains of the pith discs are projected with an optical enlarging apparatus on paper. The enlarged image may then be traced in pencil. It may be helpful to stain them say with methylene blue. The tracings can then be cut out and weighed or the area can be measured with a planimeter. The area or weight eaten can then be computed by difference from measurements of uneaten discs. One of the convenient features of this method is that the pith discs from the experiments can be mounted in a note book with cellulose tape and stored for reference.

Japanese elder pith is soft when moist and permits very good simulation of the physical characteristics of the host leaves which may in fact be cut with the same die and included as positive controls in the experiments. Blank elder pith discs are of course necessary as negative controls.

Methods for Isolating Feeding Stimulants

If there are good reasons to suspect that a known chemical constituent of the host plant may be a feeding stimulant it is probable that methods of preparations may be found in Klein's Handbuch der Pflanzenanalyse (1932). A comprehensive list of plants and their chemical constituents is given by Wehmer

(1932). Unless, however, there is a definite correlation between the botanical distribution of a chemical and the host range of the insect there is little basis for inferring a causal relationship, and even then a mere correlation must be confirmed by critical experiment.

If there are no clues as to the identity of the feeding stimulant it is necessary to pursue a strictly empirical approach and every step in the extraction of plant material and subsequent treatments must be evaluated by testing the fraction as to power to induce feeding, by one of the methods outlined earlier or otherwise.

Extraction and Purification of Phagostimulants

If, as in the host relations of *Pieris* and *Plutella* there is a known, clear-cut correlation between the distribution of certain chemicals among plants and the host preferences of the insect it may only be necessary to follow previously standardized methods of chemical preparation. However, some of the older methods of preparation may be simplified by the use of modern aids such as chromatography. For example, the mustard oil glucoside sinalbin may be adsorbed on alumina from alcoholic extracts of white mustard seed. This substance is an indicator and turns bright yellow on the usual grades of alumina so that it can be easily located and separated (Thorsteinson, 1953).

If there is no reason to suspect any of the known constituents of the host plant as the feeding stimulant it is necessary to discover the most suitable solvent for making the first extraction of the plant material. The criterion of a good solvent is, of course, that it will extract as much as possible of the feeding stimulant and at the same time as little as possible of the inactive constituents. Since this choice is very largely empirical, the only guide is to try first solvents that have been useful in previous studies of this kind. For example, sinigrin was extracted with 75% aqueous acetone (Herissey and Boivin, 1927), and sinalbin with 95% ethanol (Van Rijn and Dieterle, 1931). The feeding stimulant in the potato may be extracted with 50% ethanol from dried, powdered leaves (Chauvin, 1952) or with 65-70% ethanol from the fresh frozen leaves. I found that pure methanol is an excellent solvent for extracting fresh leaves. The extractions are of course made with boiling solvents preferably under reflux and it may be worthwhile to extract the same material twice each time with a volume of solvent in mls. equivalent numerically to three or four times the weight of the plant material in gms. If the starting material is seeds it may be desirable to remove oils by preliminary extraction with benzene.

Naturally these extracts must be presented to the experimental insects to determine their activity as feeding stimulants. Assuming that an active extract has been obtained, the next step is to fractionate it in some way so that inactive constituents may be discarded and the purity of the active fraction increased step by step to the point where it may be subjected to crystallization or otherwise isolated in pure form.

Although chromatography is peculiarly suited to the analysis of unknown mixtures it is usually most profitably employed after preliminary purifications by means of older methods which are described in various handbooks such as that of Lassar-Cohn (1928). The simplest and most effective of these depends on differential solubility in various solvents. The first extract is divided into portions of about 50 mls. and each is dried in an evaporating dish on a water bath. Each portion may then be extracted with a different solvent until a solvent is found that yields a further separation of active and inactive fractions as determined by feeding tests. There is no direct method of standardizing the concentration of the active material, but Chauvin (1952) gives a procedure for taking

this into account.   By repeating this process one can obtain a highly concentrated preparation which however may contain some impurities.

In his work on the potato beetle, Chauvin alternately extracted and dried his preparations with various strengths of ethanol.   This is a tedious procedure requiring numerous steps.   In a search for a more simple procedure I found that it is more efficient to vary the chain length of the alcohol than to vary its aqueous concentration.   The most useful alcohols are the first three in the homologous series, *viz.*, methanol, ethanol and propanol.

At this stage, chromatographic separation is worth investigation.   An excellent introduction to this technique has been provided by Williams (1946) which may be consulted for details of procedure especially for his rapid method.   A more recent and comprehensive work is that of Lederer and Lederer (1954).

An essential requirement of an adsorbent is that it temporarily adsorbs the constituent required but releases it readily to a suitable eluent.   Alumina failed to satisfy this requirement in attempts to isolate a feeding stimulant from potato leaf extracts.   Chauvin tried several other adsorbents and I tried others.   All of these either do not adsorb the active constituent or adsorb it so strongly that no eluent can remove it without destroying its activity.   The commercial availability of powdered cellulose specially prepared for chromatography finally provided a suitable adsorbent.   A useful feature of cellulose is that it is available both in powder and paper form.   Recently, we are finding that separations on paper of the old "capillary analysis" type, not to be confused with modern paper partition chromatography, provide an exceptionally useful procedure for simple and rapid separations of extracts on a small scale.   When satisfactory separations are achieved on paper they can be followed up by larger scale preparations in columns of powdered cellulose.   The ideal adsorbent for this work would be one that can itself be used as an artificial leaf.. Filter paper would serve this purpose for some insects such as wireworms but nothing suitable has been found for work with leaf eating insects.

Collection and Storage of Plant Material

As has already been mentioned, the discovery and preparation of feeding stimulants from plant extracts requires that each fraction must be tested for activity in terms of insect feeding responses.   This means that both the chemical and biological phases of the work must proceed together at least during the preliminary stages of the investigation.   For this work, fresh leaves are generally available during the active season of the experimental insect and these may be used as starting material for extraction.   When the feeding stimulant has been isolated in relatively pure form and some of its properties are known it becomes desirable to devote special attention to improving the method of preparation and purification.   To facilitate this it may be desirable to have available a supply of preserved plant material.   Chauvin (1952) advocates drying potato leaves in an oven.   This serves the purpose well, but it may not be generally applicable as there is some risk of altering the chemical plant constituents.   A simpler method is to freeze the leaves in paper bags immediately after they are collected and keep them frozen until used.   If the bags are not moisture proof the leaves will gradually dry under these conditions but in any event they will keep in excellent chemical condition.   The only disadvantage of this method is that the moisture content of the leaves is not standardized but allowance may be made for this in selecting and preparing solvents.

A further consideration regarding plant material for extraction is that feeding stimulants occur in more than one part of the plant.   Although leaves

are the parts typically eaten by insects it is not unusual to find that the seeds or the flowers yield highly attractive extracts and may be richer sources of feeding stimulants. For example, mustard oil glucosides are usually best obtained from cruciferous seeds and the flowers of sweet clover yield active extracts that contain fewer impurities than leaf extracts. Seeds present no storage problem and flowers may be dried or frozen like the leaves.

Discussion

Although the main topic of this paper concerns methods, these can be of little interest without an indication of the kind of results that they can produce and some discussion of their interpretation.

There has been some controversy, reviewed by Dethier (1954), over the question whether host plant selection is primarily guided by token stimuli (e.g. sinigrin) which have no significant nutritional value or whether the insects are guided by some kind of perception of plants that contain a satisfactory complement of nutrients. It is inevitable that the thinking of those who favor one hypothesis over the other will be conditioned by their experience in the study of particular insects. The use of experimental methods such as those described in this paper promises to supply the data needed to settle this question.

There can be no doubt that the case for the operation of token stimuli is abundantly established in several insects that have already been mentioned. A clear cut feeding response has been obtained when token stimuli are offered to these insects in a suitable experimental medium. It is significant however that these feeding responses to token stimuli in the absence of nutrients are sometimes erratic and do not compare with the quantity of feeding that occurs when fresh leaves of a normal host plant are offered.

In a preliminary analysis of this aspect of feeding behaviour in the diamond-back moth, *Plutella maculipennis*, I found that it is possible to induce a feeding response from this insect equivalent to that obtained with leaves of a favored host plant by offering a standard nutrient diet in combination with the token stimulus (sinigrin) (Thorsteinson, 1953). In fact, this insect does not give an appreciable feeding response to the token stimulus in the absence of nutrients.

Leptinotarsa is somewhat less amenable to experimental study of feeding responses but there is some evidence that its feeding responses to the token stimulus can be enhanced by the addition of certain nutrient substances such as sugar and extracts of a pharmaceutical nutrient supplement (Thorsteinson, unpublished data).

The sweetclover weevil, *Sitona cylindricollis* has proved to be rather intractable in that several attempts to enhance the attractiveness of the phago-stimulants by adding nutrients have failed. Nevertheless, it has been possible to prepare relatively pure extracts from sweet clover leaves and flowers that induce unmistakable feeding responses provided that the treated artificial leaves are mounted in such a way that the insect is free to chew notches from the edges in their characteristic way.

Olfactory Token Stimuli

It will be noticed that the discussion to this point has been concerned only with gustatory phagostimuli and it is remarkable that the main feeding stimuli for *Euproctis, Pieris, Plutella, Leptinotarsa* and *Sitona* are of the gustatory type. It has been reported, however, that acetaldehyde, an odoriferous substance, also stimulates feeding in *Leptinotarsa* (Hesse and Meier, 1950). Furthermore, Dethier (1941) induced feeding on filter paper by *Papilio* larvae with several odoriferous substances, although the possible role of purely gustatory substances

was not investigated.   Again, I was able in some experiments to enhance, slightly but significantly, the feeding response of *Plutella* to diets containing sinigrin and nutrients by adding a little mustard oil which has a very characteristic pungent odor (Thorsteinson, 1953).

On the other hand, I was unable to improve the attractiveness of test diets for *Sitona* by adding coumarin, a well known perfume constituent of its host plant, sweet clover.   There is, however, some evidence that coumarin plays an olfactory role in the feeding of *Sitona* as a food finding guide.   Professor J. D. Truscott (verbal communication, 1954) has observed that alfalfa growing at some distance from sweet clover seems to be less severely attacked than alfalfa nearer stands of sweet clover, presumably because the weevils will orientate to sweet clover over the shorter distance possibly in response to the odor of coumarin. It seems likely that acetaldehyde and mustard oil may also be of greater significance as food finding stimuli than as feeding stimuli in *Leptinotarsa* and *Plutella*. If this is so, they are more significantly related to oviposition behaviour of the adult females than to feeding of larvae.

It should now be evident that there is no single formula for the explanation of feeding behaviour of phytophagous insects in terms of the relative importance of gustatory and olfactory token stimuli and perception of nutritional substances in food plants.   Most of the evidence favors acceptance of gustatory token stimuli as the primary factor.   Olfactory token stimuli vary in importance among the insects that have been studied.   The perception of the tastes and possibly odors of nutritionally important constituents undoubtedly plays an important part in the complex of stimuli that govern normal feeding.   There is as yet little clear-cut basis, however, for the hypothesis that insects can detect and select plants that contain a complete complement of necessary nutrients.   There is some danger here of confusion over the distinction between host selection and insect infestation.   Naturally, when insects choose the most favourable host plants they tend to increase in numbers, whereas, if they select nutritionally inadequate host plants as Chin (1950) has indicated may occur, they fail to flourish and their error is not likely to be observed by investigators.

Conclusion

Host selection and the quantitative aspects of feeding by phytophagous insects are amenable to considerable experimental analysis by the techniques described.   Studies of this kind are of considerable interest to the student of insect evolution and physiology and have a potentially great application to practical problems of insect control.   One interesting possibility arises when the foreign introduction of an insect for weed control is under consideration (Holloway and Huffaker, 1952).   Will the insect attack useful plants as well as the weed?   While insect records and rearing experiments may provide a reliable answer, a knowledge of the physiology of host selection would increase confidence in the decision.

Another application of considerable promise is in the breeding of insect resistant crop plants.   For example, there is in progress at Manitoba a study of sweet clover species and varieties as genetic material for the breeding of a sweet-clover weevil resistant variety.   As some of the more promising selections happen to be low in coumarin content, there was a possibility that this substance is the key to this breeding problem.   However, since alfalfa, which contains no coumarin, is sometimes severely attacked and our experiments with artificial leaves ruled out coumarin as a feeding stimulant it became evident that one or more other constituents of sweet clover are significant factors.   Preliminary

results indicate some parallel with the feeding behaviour of *Leptinotarsa* in that the feeding stimulants are associated with flavone glucosides. Although it is undoubtedly possible to develop an insect resistant variety effectively on a purely empirical basis it is obvious that a precise knowledge of the mechanisms of insect resistance is of value in such a plant breeding program.

Considerable work, reviewed by Painter (1951), was done in Europe on potato breeding for resistance to Colorado potato beetle but, after the introduction of DDT, interest in this field diminished for a time and we may judge from this that insecticides will tend to discourage this approach to most insect problems that can at least temporarily be disposed of by chemical control. On the other hand the Colorado potato beetle in some areas appears to be developing resistance to insecticides and there is a renewal of interest in the physiology of the feeding behaviour of this insect in relation to breeding for insect resistance. Dr. R. Kuhn and his associates at Heidelberg have studied the mechanism of potato beetle resistance in certain solanaceous plants and have isolated alkaloidal glucosides such as demissin that have proven to account for failure of this insect to thrive on them. Their experiments do not answer the question as to whether demissin is toxic or unpalatable or both. I have obtained some evidence that suggests that demissin somewhat decreases palatability of artificial leaves (pith sections) treated with a feeding stimulant. This confirms similar results obtained by Langenbuch (1952). This does not, however, rule out a possible toxic action. Some progress (reviewed by Painter, 1951) has been made in producing promising hybrids of the potato with its insect resistant wild cousins. These hybrids contain demissin which is poisonous but the commercial potato also contains a similar toxic alkaloid, solanin. Therefore this is not necessarily an obstacle to success in this work.

For some insect pests such as leafhoppers and grain aphids, chemical control is difficult or impractical and plant breeding is possibly the only alternative to cultural control. It seems reasonable to conclude that an extension of our knowledge of the physiology of host selection by phytophagous insects will be profitable.

Finally it may be observed that it is hardly possible to make critical experimental studies of the nutritional requirements of oligophagous and monophagous insects until the stimuli that induce feeding are defined.

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Some Milestones in the History of Insect Classification

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Our present day concepts of the classification of insects are the result of a long period of development in the observations and thinking of the early naturalists, zoologists, and in more recent times, the more specialized entomologists. We are now so far removed from the original concepts on which the early classifications were based that many of us fail to realize that the systematic arrangement of animals, and particularly the invertebrates, was long a difficult and complicated problem which gave rise to much confusion. It may, therefore, be profitable as well as interesting to review the development of insect classification with respect to the ideas that have had a profound influence on the subject, and the men who have proposed these ideas and exerted the greatest influence. So, I propose to attempt to examine, evaluate and report to you some of the more important ideas and episodes in the development of this phase of insect taxonomy.

When we look back into the far distant past the earliest recorded ideas on the subject that are available to us are those of Aristotle (384-322 B.C.). Most historical accounts of the history of entomology briefly mention Aristotle as the first naturalist to record his observations on insects and if a more extended account of his contributions is given, an outline is often included which purports to represent Aristotle's ideas on insect classification. This was first done by Kirby and Spence in their "Introduction to Entomology", published in 1826 and has been copied extensively by other authors. Kirby and Spence attribute a classi-

fication of insects based on wing characters to Aristotle. It is true that Aristotle did mention the differences in wing characters of certain groups of insects, and if one limits the concept of an insect to our present day views, Kirby and Spence may be said to be correct. Actually Aristotle's concept of insects included a large part of the invertebrate animals and was much more comprehensive than our present concept of the term.

There has been some controversy as to exactly how Aristotle did define insects, but if one examines his work carefully, it is clear as to what he means, although it must be admitted that at times he makes some confusing statements. First of all, Aristotle divided all animals into two main groups which he called "Sanguineous" or those animals with blood, and the "Exsanguinous" or those without blood. Apparently he regarded all animals that did not have *red* blood as "Exsanguineous". Book four of the "History of Animals" treats of the "Exsanguineous" ones and at the beginning Aristotle divides them into four groups. Group one included squids, octopi and cuttlefish; group two included the higher crustacea, lobsters, shrimps and crabs; group three included the snails and clams; and group four the insects. Aristotle also suggested that animals could be classified in other ways; for example, he said that animals could be divided into those which live on land and those which live in water. This idea was later used by Aldrovandi in the first formal classification of insects.

Aristotle's definition of an insect raised a question which remained unanswered for something more than two thousand years until the present day solution was arrived at by Latreille approximately one hundred and twenty-five years ago. That question is "what animals are to be included in our concept of the term 'insect' and what are to be excluded". Aristotle used the Greek word "entoma" when he spoke of insects and in one place he attempted to define what he meant by the word "entoma"; in doing so he used the plural of the same word to indicate what he meant. The Greek word "entoma" can be translated into English as either "segments" or "divisions" so that the usual translation of Aristotle's definition is "by *entoma* I mean those animals which have divisions in their bodies". The word "entoma" apparently had other meanings in the Greek language. My former teacher, the late Dr. O. W. Oestlund used to tell his classes that the Greeks used the word "entoma" to indicate a sacrifice which had been prepared on an altar by cutting circular incisions around the animal with a knife, so that there was a series of such circular incisions from front to rear. Later they used the word "entoma" to mean an insect because of the similarity in appearance between such a prepared sacrifice and a segmented animal. An attempt to document this statement has so far met with no success. It is evident from the comments made on insects by Aristotle throughout his book that he meant to include all segmented animals under the designation "entoma".

While no formal classification of animals can be attributed to Aristotle he did make numerous suggestions as to characteristics which could be used for grouping animals together. The early naturalists including Gesner, Aldrovandi, Wotton, Moufet and others used these suggestions extensively in their published works, and some of them in modified form are still with us today.

It is well known that the subject of natural history suffered a loss of interest for a period of almost 1800 years and that when men became interested in the subject again they turned to Aristotle for information and ideas. One of the first to do this was Conrad Gesner (1516-1565) who would likely have been the first to propose a formal classification of insects had he not died suddenly from the plague before his manuscript was published. Actually this work on insects was begun in 1550 by Edward Wotton and after his death was continued

by Gesner. When Gesner died, the manuscript went to Dr. Thomas Penny, an English friend of Gesner's, who attempted to complete it but did not do so before he died in 1589. Penny's partner and executor was Thomas Moufet who brought the work to completion but did not publish it. Finally the manuscript was bought by Sir Theodore Mayerne who published it in 1634 under Moufet's name as "Insectorum sive Minimorum Animalium Theatrum" with the statement that it had its beginnings with Wotton, Gesner and Penny. No formal classification was presented in this work, although naturally certain animals were grouped together in chapters for discussion. The concept of an insect was as broad as Aristotle's and included all the segmented invertebrates.

In the meantime, the Italian, Ulysses Aldrovandus (1522-1607) had published his famous work "De Animalibus Insectis Libri Septem" in which an outline or key for the classification of insects appeared for the first time. Aldrovandi's term "Insectis" is the Latin equivalent of the Greek "entoma". He included practically all of the invertebrates under his term "Insectis" and even a vertebrate which appears to be segmented is included with a picture. It is a seahorse. Practically all of the ideas expressed in Aldrovandi's outline are to be found in Aristotle. The main division is on the basis of habitat, on land or water; secondary divisions are with feet and without feet, and finally when he treats of insects as we conceive of them today, he used wing characters just as Aristotle did and just as Linnaeus did after him. Dr. Charles E. Raven, a noted biographer of John Ray, states in his 1951 Gifford lectures on Science and Religion (1953) that Aldrovandi was a rival of Gesner and that he copied largely both text and pictures from Gesner, although he never quoted him by name or acknowledged his debt. I have not been able to verify this, but it is Dr. Raven's opinion that Gesner should be credited with inaugurating a new era in natural history and that the growth of natural sciences in the last several hundred years began with Gesner's work. Whether this be true or not the publication of Aldrovandi's book posed again the problem of what to include under the term "insects".

Aristotle knew that caterpillars grow into butterflies but he apparently did not know that butterflies laid eggs which hatch into caterpillars, because he says that "caterpillars originate in the leaves of green plants, that at first they are smaller than millet, afterward they grow into little worms, in three days they become small caterpillars, afterward they grow and become motionless and change their form. In this state the creature is called a chrysalis. After a short time the covering is burst and a winged animal escapes which is called a butterfly." Thus, we see that the bare facts of the metamorphosis of the butterfly with the possible exception of the egg were known in Aristotle's time.

Swammerdam (1637-1680) was the first to make an exhaustive study of the metamorphosis of insects and to organize the knowledge of the subject in a systematic way. His first published work on this subject, "Historia Insectorum Generalis" appeared in 1669. He proposed to arrange insects according to their method of metamorphosis. He recognized four categories of metamorphic changes in insects which he called orders. His first order which he designates as the most simple included the louse, bedbugs, spiders, mites, scorpions, centipedes, water fleas, snails, leeches, and worms of various kinds. It will be seen from this that he made very little change towards restricting the concept of insects and that most invertebrates were still included under this term. His second order included all the insects we ordinarily place as having gradual and incomplete metamorphosis. The third order included all the insects with complete metamorphosis except the higher diptera; and the fourth order included all the higher diptera or those enclosed in a puparium.

He explained the metamorphosis of an insect on the basis of the preformation theory as follows: "The nymph, or chrysalis, may even be considered as a winged animal itself hid under this particular form, from whence it follows that in reality the caterpillar or worm is not changed into a nymph or chrysalis nor to go a step further the nymph or chrysalis into a winged animal, but that the same worm or caterpillar which, in casting its skin, assumes the form of a nymph or chrysalis becomes afterwards a winged animal. Nor indeed can it be said that there happens any other change on this occasion than what is observed in chickens from eggs which are not transformed into cocks or hens but grow to be such by the expansion of parts already formed." The same concept was expressed by Linnaeus almost 100 years later much more briefly: "The metamorphosis in many insects is three-fold and consists in a change of structure effected by the subject casting the different coats in which the perfect insect is included and as it were concealed." On the other hand Swammerdam rejected the idea of spontaneous generation after learning of the experiments of Redi. Aristotle had recorded that many insects (invertebrate animals) arise spontaneously from mud, filth or some other medium. Swammerdam states unequivocally that all insects proceed from the egg which is laid by an individual of the same species.

It is also interesting to note that none of the terms we use now to designate the stages of complete metamorphosis such as larva, pupa, and imago were in use at Swammerdam's time. The immature insect hatching from the egg was known as a caterpillar if it was lepidopteran but as a worm if it was not. Aristotle used "chrysalis" for the pupa of butterflies, "aurelia" for certain pupae which had a golden color, and "necydalis" for the pupae of a silk producing insect native to the island of Cos. Swammerdam showed that a chrysalis, aurelia, and necydalis were actually all the same thing, the last immature stage of an insect, and proposed the term nymph as a substitute for all three and as a general name for this last immature stage. It was not until a hundred years later that Linnaeus introduced the term larva (since it masked the complete insect within) for the immature stage hatching from the egg and the term pupa as a substitute for nymph, chrysalis, aurelia and necydalis. Pupa was suggested because it had been used to designate a babe wrapped in swaddling clothes and Linnaeus thought he saw a resemblance between a pupa and such a child. The term "imago" was first used by Linnaeus in the 12th edition of "Systema Naturae" (1767).

While Swammerdam grouped the invertebrates according to types of metamorphosis he contributed little to limiting the concept of the term "insect". The concept at the time he died was as broad as it had ever been. He did contribute a tremendous amount of information concerning insect development, clarified this whole field, and directed attention for the first time to the importance of metamorphosis as a character useful in insect classification.

The idea that metamorphosis might be a character useful in insect classification was seized upon by John Ray (1608-1705). Ray was a botanist, but Francis Willughby who was primarily interested in insects was associated with him for a number of years. Willughby died before anything on the insects was published and later John Ray published a classification of insects based upon Willughby's manuscript. This was his "Methodus Insectorum" published in 1705. The primary divisions in his classification are based on metamorphosis. The secondary divisions are based on the presence or absence of feet and the tertiary divisions on habitat, terrestrial or aquatic. If one analyzes Ray's classification it will be seen that still no progress had been made in reducing the number of invertebrates assigned to the insects. It is true that the vertebrate sea horse and a few of the invertebrates such as the star fish had been eliminated but snails, worms of all

kinds, crustaceans, spiders, ticks, mites, and others are still included.   In fact, there is reason to believe that Ray took Aldrovandi's classification and did little more than to superimpose Swammerdam's four orders of metamorphosis upon it. Thus by the time Linnaeus appeared on the scene and began to publish, some 200 years had passed since Gesner's time.   During all of this period the term "insects" included all the segmented invertebrates, as well as some parasitic worms. The number of known animals and plants had also increased tremendously as a result of intensive world exploration, and confusion multiplied because of the lack of any method for the systematic arrangement of the living world and because of the length and awkwardness of plant and animal names.

These last two obstacles were overcome by Linnaeus when he introduced and established the use of binary nomeclature, and the systematic arrangement of animals and plants in definite ranks or categories.   The use of the definite categories, Class, Order, Genus and Species was proposed and used by him in all the editions of Systema Naturae beginning with the first in 1735, but the use of binary nomenclature was not consistently followed until the 10th edition of Systema Naturae in 1758.   Both of these techniques contributed significantly to orderly thinking about animals and plants, even though it was found desirable years later to establish two additional primary categories, phylum and family.

Linnaeus defined insects as follows: "Insects are small animals having many feet and breathing through pores arranged along their sides.   Their skin is of a hard or boney consistence.   They have moveable antennae on the head which are endowed with a sense of feeling.   The body is composed of a head, trunk, abdomen and limbs.   The head is, for the most part, distinct from the trunk.   It is furnished with eyes, antennae and, in general, with a mouth but wants brains, nostrils and ears.   The eyes are mostly two in number without eyelids.   They are either simple or compound, wings either two or four."   By defining insects thus he was able to remove a considerable number of animals formerly regarded as insects to the new class Vermes which was defined to include parasitic worms, annelids, leeches, molluscs, star fishes, hydra, volvox and others.   His class Insecta, however, still included mites, spiders, scorpions, crustacea, centipedes and millipedes.   In other words, it was equivalent to our present day phylum Arthropoda.

Having removed a considerable number of invertebrates formerly known as insects to the class Vermes there remained a number of wingless forms, but so few in comparison with the number of winged forms that Linnaeus was able to use the number and character of wings as the basis of a classification.   This was not a new idea; it had been suggested by Aristotle and was used by Aldrovandi in his outline, but both gave it such a subordinate position that its fundamental importance was obscured.   By removing a large number of heterogeneous forms from the concept of Insects and setting up a new concept Vermes to include them, the importance and uniqueness of wings in insects was emphasized and their usefulness for taxonomic purposes was established.

The introduction and establishment of binary nomeclature and of definite primary categories of classification proved a great stimulus to the cataloguing and describing of new species and genera of insects from all parts of the world. Ultimately this led to changes in classification and the establishment of new orders of insects.   This was the one great achievement for both botany and zoology during the 18th century and it may be that biology had reached a point where it could advance no further until this had been done.   Many writers after Linnaeus wrote of him in most extravagant terms.   To quote from Kirby and Spence, "Such were the services rendered to entomology by the labors of the

immortal Swede; services so extensive as well as eminent, that had they been the fruit of a whole life devoted to a single object they would have entitled him to a high rank amongst the heroes of the science . . . It is not so much in original discovery that the merits of Linnaeus lie as in the unrivalled skill with which he sifted the observations of his predecessors separating the ore from the dross and concentrating scattered rays of light into one focus".   A more recent evaluation by Dr. Charles E. Raven, the eminent biographer of John Ray, while seeking to give Linnaeus his due is more critical of him as a scientist, "Linnaeus has received so large a meed of honor both in his own day and subsequently, has become so generally regarded as the chief founder of botanical and zoological studies, and has left behind so rich a legacy both of learning and of legend that it is important to understand his precise place in the development of science.   This as he himself understood it he has made abundantly plain.   When his disciples printed the motto 'Deus creavit, Linnaeus disposuit,' under his portrait we may question their taste but cannot mistake their claim.   For him, classification, the arrangement and naming of species is science and he is the great classifier.

"As such it is easy to underestimate the scale and value of his work.   Binary nomenclature had been foreshadowed both in botany and zoology by several of his predecessors and as known species became more numerous and the alternative to the system was the use of longer and more elaborate descriptions, its convenience was evident.   But full credit must be given to Linnaeus for adopting it as a universal principle, and for the skill and fertility of invention with which he applied it.   In his day when the simple definition of a species as that which proceeded at the creation from the hand of God was generally accepted, and when there was no need for elaborate rules of priority and no cleavage between botanists and zoologists in their elaborations of his system, the result had an immense value in giving clarity and simplicity to nomenclature.

"He encouraged his pupils to travel very widely; he sought for specimens whether by gift or loan or purchase from a vast circle of correspondents; he promoted the formation of museums and fostered the collector's passion wherever he could; and he devoted his time without stint to the business of scrutinizing, naming and cataloguing the resultant specimens.   No single person before him had amassed any comparable series of pressed plants, preserved insects, fishes and reptiles, bird skins and eggs, and the skins and bones of mammals; and he had seen and named far more than he possessed.   Material was thus available for him as it had not been for any earlier naturalist, and in sorting, describing and naming it, he showed a remarkable accuracy and skill.   His particular abilities lay precisely in this direction.   He had no concern with philosophy or with ultimate questions: the very word 'philosophy' on his lips meant little more than the compilation of an appropriate vocabulary.   He had little interest in anatomy or physiology except so far as to recognize that difference of structure might be important for identification.   He hardly shared Ray's desire to see the living plants and birds in their natural environments or his flair for observing peculiarities of habit or behavior.   For nomenclature, however, he had a real passion and to add new items to his lists was the quest of his life.   Regarding the naming of plants and animals as Adam's chief prerogative and occupation in Paradise he found a sacred calling and a source of boundless pride in his own similar task.   His skill in noting, and his clearness in defining differences gave his work a high and permanent value. In a very real sense he initiated a new epoch in botany and zoology by discriminating and naming so wide a range of species.

"Unfortunately, his appetite for fame which in later life became almost overweaning, made him contemptuous of any other form of biological science.

Thus his strictures upon Ray, from whose work he borrowed largely but with scanty acknowledgment, reveal both his conviction that the fundamentals of botany were nomenclature and classification; and his failure to realize that classification must be based upon truly structural characteristics. Anyone who was not content merely to describe and name, anyone who treated taxonomy as a matter rather of convenience than of profound importance was dismissed by him as no true scientist. As he acquired an almost legendary reputation and until the present day has been treated with a reverence out of proportion to his merits, his influence upon the development of biology has been by no means as beneficial as is commonly assumed."

John Christian Fabricius, a student of Linnaeus, may be said to have been the first entomologist in the sense that he devoted his scientific efforts exclusively to insects. He never realized his ambition to be a teacher of entomology but was compelled by force of circumstances to accept a professorship of economics at the University of Kiel which he held during all his active career. Nevertheless, his primary interest was in insects and a significant part of his time was devoted to them. He travelled extensively in all parts of Europe and was personally acquainted with most of the students of insects of his day. His principle contribution to insect classification was to propose an entirely new and different classification than that of Linnaeus based on the structure of the mouthparts and particularly the maxillae. Ultimately his proposal came to be known as the maxillary system. The Linnaean definition and concept of "Insect" remained unchanged and still included all the animals which we think of as Arthropods. Actually his proposal involved the increase in number of orders from seven to thirteen and redefining the orders in terms of mouthparts without in any way changing the concept of the word "Insect".

The deficiencies of the Linnaean alary system and the Fabrician maxillary system served to emphasize the point that a natural classification cannot be based on the characters of a single morphological structure, but at the same time each of them focussed attention on a single set of structures which were of fundamental importance and neither of which could ever be ignored in the future in insect classification.

The restriction of the class Insecta to animals with three distinct body regions, three pairs of legs, and usually two pairs of wings was brought about by three eminent French workers in the early part of the nineteenth century. The difficulty of accomplishing this is emphasized by the fact that three such eminent zoologists and entomologists as Lamarck, Cuvier and Latreille were occupied with the problem for something over thirty years. All three were concerned regarding the establishment of a natural system of classification of animals, one which would take into account not only one morphological structure but all structure both external and internal, metamorphosis, respiration, feeding habits, in fact the animal as a whole, and which would indicate relationships on such a basis.

Latreille first attempted this in 1796 in a work entitled "Précis des Caractères génériques des Insects, disposés dans un ordre naturel." Although all the Arthropods are still regarded as insects he states that he has made an attempt to indicate natural relationships by the grouping of genera into families. This is the first proposal to establish the primary category family between that of Order and Genus. Whether this was original with him or suggested by Cuvier or Lamarck cannot be determined. He was on friendly terms with both, and acknowledges aid from Cuvier and others in the preface to the "Précis". With reference to the category family in this work he states, "The anatomical resemblances, those

of habitus, of metamorphosis, have been my guide in the formation of families. One might desire that I should have given names to the families; but conscious that I would be compelled to make many changes, I would thus have exposed nomenclature to a vicissitude very adverse to the advancement of science."

The Crustacea were first elevated to the rank of class by Cuvier in 1799, although only a part of the presently recognized Crustacea was included. Lamarck in 1801 not only expanded the class Crustacea to approximately its present limits, but also proposed a new class Arachnida to include the scorpions, spiders, millipedes, centipedes, Collembola and others. While both the Crustacea and Arachnida were thus proposed as new classes at the turn of the nineteenth century, the definition of both was such as to cause confusion for the next two decades. The Crustacea were defined by Cuvier to include only the higher forms, the Malacostraca, while Lamarck went to the opposite extreme by including Thysanura, Collembola, the lice and Myriapoda in his class Arachnida.

Latreille's "Histoire Naturelle, générale et particulière des Crustacés et Insectes" appeared in 1802. This may be said to be the first textbook in entomology since it includes chapters on insects and other invertebrates, nutrition, mouthparts, means of defense, insect habitations both solitary and social, instructions for collecting and preserving specimens, colors of insects with a table of classification of colors, the usefulness and destructiveness of insects, internal and external anatomy, reproduction, metamorphosis, and an analysis of all the classificatory systems that had appeared up to the time of publication. Latreille's classification as published in this work accepts Cuvier's class Crustacea which excluded Entomostraca, but rejects Lamarck's class Arachnida, so the class Insecta still includes everything but the higher Crustacea. It was in this work that Latreille first gave names to the families.

The Crustacea, excepting the terrestrial Isopoda, were recognized as a class in "Genera Crustaceorum et Insectorum" (1806) and everything else included as Insects. The Arachnida were recognized as a class by Latreille in "Considérations générales sur l'ordre naturel des animaux composant les classes des Crustacés, des Arachnides et des Insectes" (1810) but it included such diverse groups as spiders and Thysanura, millipedes and sowbugs, and sucking lice and ticks.

By 1817, in Cuvier's "Le Règne animal", Latreille had clarified the definition of the Arachnida so that the Thysanura, Parasita and Myriapoda were removed to the Class Insecta. He removed the Myriapoda from the Insecta in 1825 in "Familles naturelles du règne animal". His last work, "Cours d'Entomologie ou de l'histoire naturelle des Crustacées, des Arachnides, des Myriapodes et des Insectes" was a refinement of his views expressed in 1825 with the recognition of four classes of segmented animals with legs, the Crustacea, Arachnida, Myriapoda and Hexapoda, and the latter arranged in twelve orders.

Thus from the time of publication of Aldrovandi's work to this last work of Latreille, a period of some two hundred and twenty-five years there was a continual effort to define the concept of an insect in such a way as to include an essentially homogeneous group of animals. It was only accomplished after a long effort, a great amount of discussion and debate, and a consideration of the ideas of many biologists, only the most outstanding of which we have mentioned.

What were the stumbling blocks that lay in the way of the achievement of a scientific classification of insects? At the beginning there were several: (1) the complete confusion existing in the minds of men regarding the parasitic worms, segmented worms and insect larvae; (2) the absence of any definite concept of a species; and (3) the lack of any framework, that could be used for grouping similar or closely related organisms together, and for separating those

that were different. The first of these was greatly clarified by the work of Swammerdam who elucidated and emphasized the differences between worms and insect larvae; the second was remedied by John Ray who was largely responsible for developing the concept of species, and the third was supplied by Linnaeus when he adopted the categories of Class, Order, Genus and Species. At least two handicaps remained after Linnaeus: (1) the persistence of the idea that a classification could be based on a single structural character; and (2) the great difficulty encountered in arriving at a satisfactory definition of the Class Insecta. The first was overcome through the combined efforts and teaching of Cuvier, Lamarck and Latreille who together and individually developed what they called a natural system; the second was slowly but surely overcome by Latreille as over the years he made more and more precise definitions of the classes, so that towards the end of his career the Class Insecta was defined and limited to approximately its present scope.

Insect classification came a long way from the time of Gesner and Aldrovandi to that of Latreille and had now progressed to a point that seemed to have achieved a goal, that of limiting the class Insecta to those invertebrates which form a closely integrated phylogenetic unit. This was the end of an era. A new era was about to begin. It was foreshadowed by Lamarck and his theory of evolution based on biological characters acquired by use and disuse. Lamarck was vigorously opposed by Cuvier.

Imagine now Latreille: associated with both at the Museum d'Histoire Naturelle, looking upon Lamarck more or less as a father, and intimate with Cuvier to the point of contributing the Insect part of his Le Regne Animal. It may well be that the delay in establishing a precise definition of the class Insecta was due to conflicts arising out of the opposing views of these great minds.

The new era was finally ushered in by Darwin with the publication of his "Origin of Species". The acceptance of Darwin's views gave new impetus to the development of insect classification and the changes that have been made since Latreille's day are entirely due to a new point of view towards phylogenetic research brought about by the influence of the theory of evolution on the minds of biologists.

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Les associations de Gyrins dans les étangs et les lacs du parc du Mont Tremblant

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L'étude monographique de H. C. Fall (1922), "The North American species of *Gyrinus*", a permis à de nombreux entomologistes de reconnaître assez facilement les Gyrins des territoires inventoriés par eux-mêmes et a facilité la mise en ordre des collections existantes. Nous en voyons la preuve dans les quelques additions ou listes qui parurent durant les dix années suivantes. Wallis (1926) décrit le *Gyrinus dubius* et le *G. hatchi*; il restaure le *G. piceolus* Blatchley qui avait été réduit au rang de synonyme par Fall. Chamberlain (1929) décrit le *G. gehringi*, provenant de l'état du New Hampshire. Brown (1928) donne une liste des espèces canadiennes. Il énumère vingt espèces pour la seule province de Québec, dont la plupart proviennent de la région de Hull ou de Covey Hill. Le *Gyrinus opacus* n'est cependant mentionné que pour la baie James. En 1931, Fall donne la description de *Gyrinus instabilis* dont le type et les paratypes proviennent de l'Alaska. Depuis, très peu de travaux semblent avoir été faits sur ce genre d'insectes, soit au Canada, soit aux Etats-Unis.

But et méthode

Dans notre étude de la faune entomologique aquatique de la région du parc du mont Tremblant, il convenait d'apporter une attention spéciale aux Gyrinidés, qui sont particulièrement abondants dans les lacs et rivières de cette partie des Laurentides. En effet, on connaissait très peu les espèces qui habitent ce territoire de la province de Québec, car rares sont les entomologistes qui en ont fait une étude intensive. Le Rév. Frère J. Ouellet, c.s.v., possédait dans sa riche collection de coléoptères nord-américains huit espèces de Gyrins recueillis à Nominingue, et treize seulement pour l'ensemble de notre province. La collection de l'Institut de Biologie de l'Université de Montréal possédait deux espèces des Laurentides et dix pour l'ensemble du Québec. D'autre part, sur les préférences écologiques des diverses espèces, sur le rôle que ces insectes jouent dans le milieu aquatique, nous ne possédions pratiquement aucun renseignement précis.

A l'origine ce projet devait se limiter à un petit nombre d'habitats aussi différents que possible les uns des autres. Ces habitats sont décrits sommairement au paragraphe suivant. A chacune de ces étendues d'eaux, nous avons réalisé plusieurs collections successives réparties sur une ou deux années. Au cours de l'été 1954, à l'occasion de la visite de nouveaux territoires, nous avons effectué des collections à plusieurs autres lacs, ce qui permet d'avoir une vue plus générale de la distribution de chacune des espèces rencontrées. Cette étude a nécessité l'examen de près de onze mille Gyrinidés. Elle a permis de retracer deux espèces dans le genre *Dineutus* et seize dans le genre *Gyrinus* sur le territoire couvert par nos travaux.

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Plusieurs collègues de la Station biologique du Mont Tremblant nous ont apporté leur concours au moment des collections. M. Albert Courtemanche, directeur de la Station, et le Rév. Frère J.-R. Mongeau, c.s.v., ont effectué eux-mêmes certaines récoltes qu'ils nous ont remises pour étude. M. W. J. Brown, entomologiste systématicien à Ottawa, a déterminé ou vérifié l'identification des huit espèces que nous lui avions soumises. M. A. Courtemanche a bien voulu

lire le manuscrit et faire d'utiles suggestions. Nous remercions vivement tous ces collègues et amis de leur aide infiniment précieuse.

Site de la Station biologique

Ces recherches sur les Gyrins furent poursuivies à la Station biologique du Mont Tremblant, qui est établie sur les rives de la rivière du Diable, à 20 milles environ au nord de la route Montréal-Mont-Laurier. Le chemin gravelé qui y conduit laisse la route principale à Saint-Faustin. Les édifices qu'occupe la Station sont érigés à cette partie de la rivière connue sous le nom de lac Monroe. A un demi-mille en aval, la rivière demeure endiguée par un vieux barrage, utilisé autrefois pour le flottage du bois.

Principaux habitats étudiés

Les habitats aquatiques dans lesquels nous avons récolté des Gyrins durant les années 1952 à 1954 sont trop nombreux pour que nous entreprenions de les décrire tous, ne fut-ce que sommairement. Seuls, nous retiendront ici les lacs où plusieurs collections successives ont été réalisées dans le but de déceler les variations ou la constance des populations de Gyrins. Ces habitats, et la plupart des autres dont nous ferons mention, pourront être localisés sur la carte ci-jointe.

Les habitués de la région distinguent parfois entre Petit Monroe et Grand Monroe. Ces lacs sont formés par des élargissements de la rivière du Diable et ne sont séparés que par un court détroit. Le niveau de l'eau sur ces lacs, à cause de l'état actuel du barrage et de la crue du printemps, varie considérablement. Au cours de 1954, les différences entre le niveau maximum et minimum ont atteint près de six pieds. De nombreuses et abondantes collections de Gyrins furent réalisées au cours de chacune des trois années, plus particulièrement dans la baie au sud de la station biologique et au voisinage du barrage. Les collections effectuées ici et là dans le Grand lac Monroe ne sont pas séparées des précédentes parce qu'elles montrent les mêmes caractéristiques.

Le lac Lauzon est un lac aux eaux extrêmement limpides et qui possède une fosse centrale de 90 pieds environ. Un lac aussi profond, qui n'est séparé de la rivière du Diable que par une bande de gravier de 500 à 1000 pieds de largeur semble bien avoir une origine glaciaire. D'après Courtemanche (1953) le lac Lauzon se trouverait au point de recontre d'une vallée glaciaire latérale avec la vallée glaciaire de la Diable. La fluctuation du niveau du lac Lauzon est réduite au minimum. Le ruisseau qui sert d'émissaire ne coule que durant quelques jours au printemps. Les populations de Gyrins sont abondantes, particulièrement en bordure de la rive nord-est. Nous avons effectué trois collections à cet endroit au cours de l'été 1952.

Le lac Brochet est situé en aval de la Station à deux milles environ de la route, sur la rive droite de la rivière. Ses dimensions ne sont pas considérables (1500 pieds par 500 pieds environ); sa profondeur maxima atteint une vingtaine de pieds. Une épaisse couche de vase recouvre le gravier. Une végétation ligneuse occupe tout le rivage jusqu'à la limite de l'eau; la zone littorale est plutôt large; les populations de Gyrins y sont très considérables à toute période de l'été. Trois collections y furent effectuées au cours de chacune des années 1953 et 1954.

Le lac Nansen est situé au nord-ouest du lac précédent. Il n'en est éloigné que par quelques centaines de verges. Ses eaux, cependant, se dirigent dans le bassin de la rivière Cachée. Ses dimensions restreintes et sa faible profondeur, 3 à 4 pieds, devraient nous amener à parler plutôt d'un étang que d'un lac proprement dit. Les deux extrémités de ce lac sont formées d'un sol tourbeux exondé, couvert de Carex et d'Ericacés. De petites sources rhéocrènes y apportent leurs

PARC DU
MONT TREMBLANT
———————
SECTEUR MÉRIDIONAL
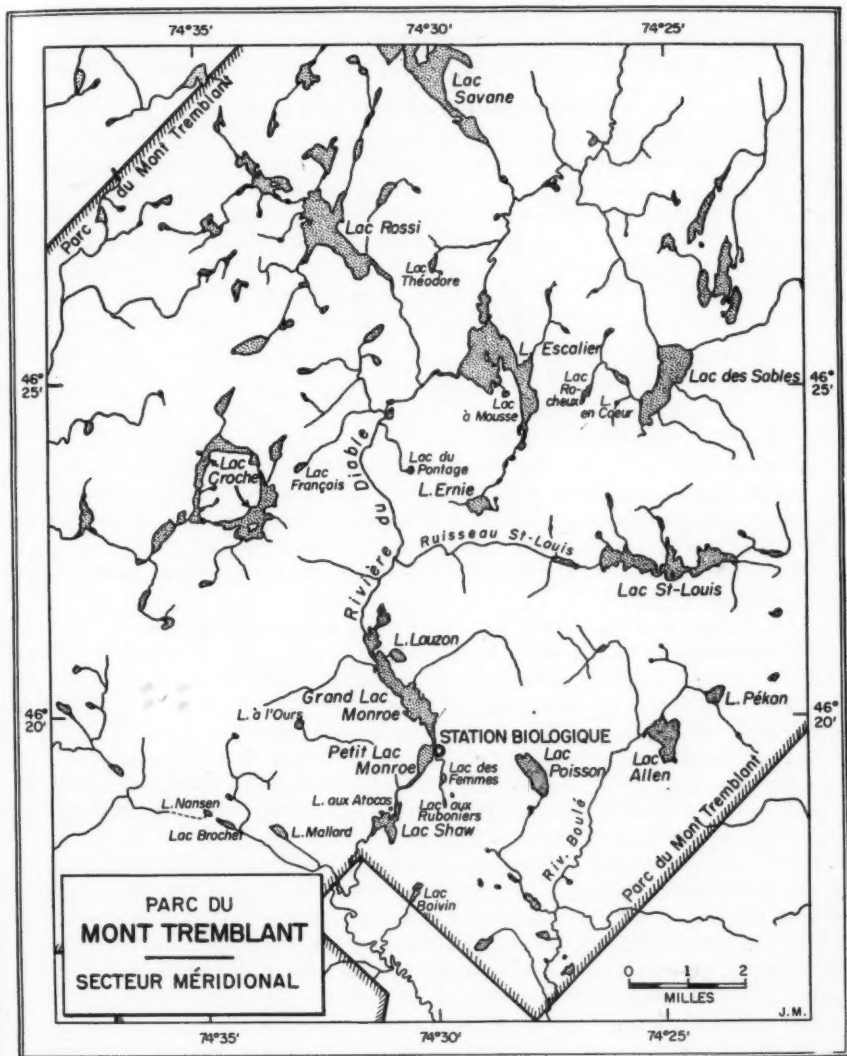
eaux et suffisent à maintenir le niveau d'eau à peu près constant. Nous y avons collectionné des Gyrins en 1953 et en 1954.

Le lac aux Atocas, sis à proximité de la route et de la rivière, à un mille au sud de la Station biologique est d'accès facile. Ses eaux brunes, relativement profondes, vingt pieds environ, et sa rive flottante, formée d'Ericacés et de sphaignes, caractérisent à merveille ce type de lacs qu'on a appelé dystrophes. Les collections de Gyrins ne furent pas aussi abondantes que dans les autres types d'habitats, mais révèlent des espèces intéressantes.

Parmi les ruisseaux visités, celui qui amène le trop-plein des eaux du lac Boivin à la rivière du Diable s'est montré particulièrement riche en Gyrins dans

le secteur adjacent au lac. Nous n'avons réalisé toutefois qu'une seule collection à cet endroit, le 1er août 1952. La collection rapportée en 1954 a été effectuée sur les rives du lac. Aucun Gyrin ne fut aperçu à ce moment dans l'émissaire.

Composition des colonies de Gyrins

On sait très bien depuis l'étude monographique de Fall, citée plus haut, que les Gyrins forment des associations d'individus qui groupent généralement plusieurs espèces. Il ne suffit donc pas pour connaître les Gyrins d'un territoire donné de recueillir quelques exemplaires de chaque colonie. Il nous est arrivé souvent de remarquer dans un échantillon tant soit peu considérable de quatre à six espèces et même davantage vivant en complète harmonie. Ainsi l'identification des 150 Gyrins recueillis le 19 juillet 1952 au voisinage de la Station biologique a révélé quatre espèces représentées dans les proportions suivantes:

Gyrinus fraternus	45 ♂	21 ♀	soit 44.0%
Gyrinus impressicollis	17 ♂	30 ♀	soit 31.3%
Gyrinus lugens	21 ♂	15 ♀	soit 24.0%
Gyrinus confinis	1 ♂		soit 0.7%

Comme on le voit, dans une colonie de Gyrins, toutes les espèces ne sont pas également réparties; les unes dominent par leur nombre, tandis que d'autres ne possèdent que quelques représentants; certaines ne comptent parfois qu'un seul individu. Pour obtenir ces dernières espèces, il faut s'astreindre, sinon à la revue complète de l'association, du moins à l'examen d'un nombre très considérable d'individus.

Au tableau 1, apparaissent les résultats des collections successives réalisées au lac Brochet. Les trois collections du 28 mai 1953 furent effectuées à des endroits distincts du lac, toutefois pas très éloignés les uns des autres. L'examen des deux premières collections, formées respectivement de 109 et 270 individus, n'était pas suffisant pour donner une idée complète de la composition des associations de Gyrins présentes à ce moment de l'année, puisque l'examen du troisième lot (306 individus) a révélé deux espèces additionnelles. La collection du 9 juin a également révélé une espèce non rencontrée précédemment; celle du 9 juillet (359 individus) a apporté le même résultat.

Au cours de l'année 1954, nous avons tâché de voir si les résultats obtenus au lac Brochet l'année précédente pouvaient être confirmés. A notre grande surprise, dès le 23 mai, trois espèces s'ajoutent aux dix espèces rencontrées en 1953. La collection effectuée le 7 juin, formée de 308 individus, n'a apporté que des espèces déjà notées. Peut-on conclure que la faune du lac Brochet en Gyrins est parfaitement connue? Peut-être. Cette connaissance, toutefois, n'aurait été acquise qu'à la suite de l'examen de plus de 1800 individus.

Il est à remarquer que ces données n'ont pas été obtenues à un seul moment de la saison, mais proviennent des collections effectuées durant deux années consécutives et à différents moments de l'été. En fait, il pourrait y avoir des variations chronologiques dans l'apparition de certaines espèces et même des variations annuelles. Nos résultats trouveraient dans ce fait une explication plausible; ils ne permettent pas cependant de prouver l'existence de telles variations de façon certaine.

Caractéristiques des colonies de Gyrins

Les trois collections de Gyrins effectuées le 28 mai 1953 au lac Brochet dans trois colonies différentes démontrent qu'il existe une certaine homogénéité de composition des colonies. Dans chacune, l'espèce *pectoralis* prédomine; l'espèce *affinis* vient en second. D'autre part, les divergences de composition ne manquent

TABLEAU I

Variation de la composition des colonies de Gyrins au lac Brochet (P. M. T.)

Numéro des collections:	1	2	3	4	5	6	7
Espèces rencontrées:	28 mai 1953			9 juin 1953	9 juil. 1953	23 mai 1954	7 juin 1954
G. pectoralis	74.3*	84.4	72.1	71.2	–	17.0	89.2
G. lugens	19.3	–	14.1	6.2	4.4	7.9	0.4
G. instabilis	–	13.0	10.8	20.4	3.3	0.3	9.7
G. affinis	2.7	2.2	1.3	1.1	81.1	5.0	–
G. dichrous	3.6	–	–	–	–	–	0.4
G. impressicollis	–	0.4	0.3	–	–	–	–
G. confinis	–	–	0.7	–	–	–	–
G. fraternus	–	–	0.3	–	–	–	–
G. lecontei	–	–	–	1.1	10.8	–	–
G. frosti	–	–	–	–	0.3	–	–
G. gehringi	–	–	–	–	–	59.8	–
G. latilimbus	–	–	–	–	–	8.3	0.4
G. pugionis	–	–	–	–	–	2.0	–
Nombre d'individus examinés:	109	270	306	274	359	241	308

*Valeurs exprimées en pourcentage.

pas; l'espèce *lugens*, relativement abondante dans les colonies 1 et 3 fait défaut dans la colonie 2.   On peut noter le même phénomène pour l'espèce *instabilis* qui ne figure pas dans la colonie 1 alors qu'elle est bien représentée dans les colonies 2 et 3.   L'espèce *impressicollis* est à peine représentée dans les colonies 2 et 3; il n'est donc pas surprenant de constater son absence dans la colonie 1.   La présence de *G. dichrous*, *G. confinis* et *G. fraternus* dans une seule des colonies n'a rien d'anormal puisque l'ensemble des collections réalisées à ce lac démontre que ces espèces sont en tout temps peu abondantes.

Les résultats qui apparaissent pour la colonie 4 cadrent assez bien avec les trois précédents puisque les espèces dominantes sont les mêmes.   Il n'en va pas de même de la colonie 5 dans laquelle l'espèce dominante est *G. affinis* et la seconde en importance est *G. lecontei*.   L'absence de *G. pectoralis* dans cette colonie reste inexpliquée, puisque comme nous le verrons dans l'examen des résultats obtenus à d'autres lacs, cette espèce n'a pas un cycle exclusivement printanier.

Les données du 23 mai 1954 font voir que l'espèce dominante dans la colonie étudiée alors est le *G. gehringi* et que la troisième en importance est le *G. latilimbus*, deux espèces qui ne figurent pas dans les relevés antérieurs.   La dernière colonie étudiée, 7, ne montre que des écarts minimes avec les trois premières.

TABLEAU II

Variations annuelles dans la composition des associations de Gyrins
dans certains lacs des Laurentides.

Espèces rencontrées:	Lac Monroe		Lac Brochet		Lac Nansen		Lac aux Atocas	
	1952–53	1954	1953	1954	1952–53	1954	1953	1954
G. fraternus	53.9*	61.6	0.1	–	–	–	–	0.4
G. lugens	22.5	17.3	4.2	3.4	21.7	17.3	21.0	21.6
G. impressicollis	18.2	9.6	0.2	–	–	–	–	–
G. confinis	1.4	6.6	0.2	–	–	–	–	–
G. latilimbus	1.1	1.0	–	3.8	4.6	21.8	4.8	6.0
G. dichrous	0.9	1.4	0.3	0.2	–	1.3	–	–
G. affinis	0.8	–	28.4	2.3	55.7	10.3	1.6	3.8
G. ventralis	0.6	2.3	–	–	0.2	1.3	–	–
G. frosti	0.3	0.1	0.1	–	0.2	–	–	–
G. bifarius	0.2	–	–	–	–	1.3	–	–
G. pectoralis	0.1	–	52.6	57.3	0.5	1.3	1.6	–
G. instabilis	0.06	–	13.7	5.8	0.2	0.6	–	–
G. pugionis	–	–	–	0.9	15.4	41.7	64.5	68.0
G. gehringi	–	–	–	26.0	0.2	2.5	4.8	–
G. lecontei	–	–	0.2	–	0.7	–	1.6	–
G. minutus	–	–	–	–	0.5	0.6	–	0.4
Nombre d'individus examinés:	3000	719	1384	550	395	156	62	236
Nombre d'espèces:	12	8	10	8	11	11	7	6
Nombre total d'espèces:	12		13		13		9	

*Valeurs exprimées en pourcentage.

L'analyse de ces résultats fait voir combien il est difficile d'obtenir une connaissance exacte de la population de Gyrins qui habite un lac, même de faible étendue. Les raisons en semblent multiples; car, d'une part, à un moment donné de l'année les diverses colonies montrent une composition différente; d'autre part, avec l'avancement de l'été, on assiste apparemment à une succession d'espèces; des espèces d'abord abondantes disparaissent plus ou moins et cèdent la place à d'autres qui ne comptaient qu'un petit nombre de représentants ou qui manquaient tout à fait; cette fluctuation saisonnière existe-t-elle à l'échelle annuelle? Cela ne semble pas impossible.

L'examen du tableau II nous convainc davantage de la difficulté d'un inventaire complet de la faune des Gyrins peuplant une étendue d'eau. En effet, l'étude de plus de 700 individus capturés au lac Monroe au cours de 1954 ne

permet pas de retrouver toutes les espèces décelées durant les deux années précédentes dans ce même lac.   Aux lacs Brochet, Nansen et Atocas, l'inverse se produit; de nouvelles espèces sont découvertes alors que le nombre d'individus examinés est parfois moindre que celui des années précédentes.

L'étude comparative de l'abondance annuelle de chacune des espèces montre moins de variations au lac Monroe qu'aux lacs Brochet et Nansen (tab. II).   Au lac aux Atocas, l'ordre d'abondance est le même pour les quatre espèces dominantes: G. *pugionis*, G. *lugens*, G. *latilimbus* et G. *affinis*; d'autre part, il est quelque peu surprenant que G. *gehringi* n'apparaisse pas dans les relevés de 1954, alors que le nombre d'individus examinés est quatre fois plus considérable.

Au début de cette étude, nous avons indiqué les caractéristiques des quatre lacs dont il est question au tableau II.   Ces lacs étant très différents du point de vue physiographique, nous étions anxieux de savoir s'ils montreraient de réelles différences dans leur faune, principalement chez les Gyrins.

Au lac Monroe, le G. *fraternus* est d'emblée l'espèce dominante; viennent ensuite G. *lugens*, G. *impressicollis* et G. *confinis*.   Toutes les autres espèces sont beaucoup moins importantes.   Au lac Brochet, l'espèce dominante est le G. *pectoralis* suivi par ordre d'abondance de G. *affinis*, G. *instabilis* et G. *lugens*. Comme nous l'avons déjà signalé, G. *gehringi* prend, au cours de 1954, une importance qu'il n'avait pas l'année précédente.   Au lac Nansen, G. *affinis* et G. *pugionis* dominent, suivis de G. *lugens* et G. *latilimbus*.   Au lac aux Atocas, G. *pugionis* est sans contredit l'espèce abondante; viennent ensuite G. *lugens*, G. *latilimbus* et G. *lecontei*.

En définitive, mis à part G. *lugens* et G. *affinis*, espèces ubiquistes, qui ne semblent avoir aucune exigence écologique ainsi que les espèces dont la représentation est plutôt faible et assez peu constante, les entités spécifiques qui apparaissent au tableau III peuvent servir à caractériser les trois types de lacs étudiés.

Il s'ensuit que les associations de Gyrins étudiées dans le parc du mont Tremblant paraissent constituées de trois catégories d'espèces que nous pourrions qualifier respectivement d'espèces ubiquistes, d'espèces caractéristiques et d'espèces secondaires.   Les espèces ubiquistes se retrouvent dans presque toutes les associations; elles figurent parfois en grand nombre mais peuvent aussi ne compter que quelques individus.   Les espèces caractéristiques de l'association se rencontrent, à peu de variantes près, dans toutes les associations de même type.   Ce sont les espèces qui dominent ou codominent par leur nombre et par la constance de leur représentation.   Les espèces secondaires de l'association bien que plus nombreuses que les précédentes du point de vue entités spécifiques, ne comptent en général que peu d'individus de chaque espèce et leur nombre global est rarement important si on le compare à celui des espèces ubiquistes ou caractéristiques.

TABLEAU III

Gyrins caractéristiques des divers types de lacs.

Lac fluvial de type eutrophe (Monroe)	Lac glaciaire de type eutrophe (Brochet)	Lac semi-tourbeux ou tourbeux de type dystrophe (Nansen et Atocas)
G. *fraternus*	G. *pectoralis*	G. *pugionis*
G. *impressicollis*	G. *instabilis*	G. *latilimbus*
G. *confinis*	G. *gehringi*	G. *lecontei*

Les espèces secondaires d'une association de Gyrins ont des origines différentes. Les unes, telles G. *dichrous*, G. *ventralis*, G. *frosti*, et G. *bifarius* peuplent surtout des régions plus méridionales. G. *minutus*, au contraire, compte de plus fortes populations sous les climats froids; sa présence dans le parc reste à peu près limitée aux lacs dystrophes.

D'autres espèces secondaires doivent être considérées comme purement accidentelles ou encore comme pionnières ou reliquales. Les espèces purement accidentelles dominent dans une autre association où le milieu biologique possède des caractéristiques différentes. Leur présence hors de leur association naturelle est une conséquence de leur pouvoir migrateur. Les espèces reliquales ou pionnières sont liées au stade de l'évolution de l'habitat et au dynamisme de la succession.

La multiplicité des étendues d'eaux dans la région du parc et la possibilité pour les Gyrins de se poser en tous lieux contribuent à faciliter leurs déplacements. Toutefois, les migrations semblent le fait plutôt de quelques individus que du grand nombre. Le sort de ces individus migrateurs qui parviennent dans un milieu dont la physiographie semble inadéquate à leurs exigences n'est pas encore connu. Des études prolongées des populations adultes et des formes immatures d'une étendue d'eau restreinte permettront d'élucider cet aspect de la vie grégaire des Gyrins.

L'examen du tableau IV permet de constater une fois de plus l'hétérogénéité des diverses associations de Gyrins dans une douzaine d'autres habitats. La recherche des espèces caractéristiques de chacun, basée sur l'abondance de leur représentation permet de ranger certains de ces lacs dans leur facies particulier. Ainsi, il ne fait aucun doute que le lac à Mousse et le lac Rocheux où dominent G. *pectoralis* et G. *instabilis* se rapprochent du lac Brochet par leur aspect physiographique. Le lac Boivin possède des affinités avec le lac aux Atocas et le lac Nansen. C'est d'ailleurs ce que nous avons pu constater au moment des récoltes. Il n'est pas toujours aussi facile à la lumière de l'étude des populations de Gyrins qui l'habitent de déceler le facies d'un lac. Il semble, toutefois, qu'une observation un peu étendue des populations de Gyrins qui évoluent sur un lac soit un excellent indice des caractéristiques de ce lac.

Liste annotée des Gyrinidés rencontrés dans le parc du Mont Tremblant

A la suite de l'étude systématique que nous avions faite des diverses collections de Gyrins obtenus dans la région du parc du mont Tremblant, nous avons tenu, étant donné l'absence de plusieurs espèces dans les collections à notre disposition et la difficulté du groupe, à soumettre à M. W. J. Brown quelques exemplaires des espèces suivantes pour vérification ou détermination: *Gyrinus pugionis* Fall (5 ex.), *Gyrinus lecontei* Fall (3 ex.), *Gyrinus frosti* Fall (2 ex.), *Gyrinus bifarius* Fall (2 ex.), *Gyrinus ventralis* Kby (3 ex.), *Gyrinus fraternus* Coup. (6 ex.), *Gyrinus gehringi* Chamb. (4 ex.), *Gyrinus instabilis* Fall (4 ex.), Au sujet de cette dernière espèce M. Brown note: "These specimens agree well with the description and three female paratypes of *instabilis*. Direct comparison of male genitalia is required." Des démarches à cette fin sont en cours. Nous remercions vivement M. Brown de sa grande bienveillance.

Dineutus horni Rbts

Cette espèce n'a été capturée qu'aux lacs Nansen et Atocas et encore que très rarement parmi d'abondantes populations de l'espèce suivante. Observé en mai et juin.

Dineutus nigrior Rbts

C'est le Dineute dominant dans la région. On le remarque surtout sur les eaux des lacs encaissés dans les montagnes, de type eutrophes ou dystrophes. Sa

TABLEAU IV

Composition des associations de Gyrins dans le parc du Mont Tremblant

Espèces rencontrées:	Lac Lauzon	Lac des Femmes	Lac à Mousse	Lac en Coeur	Lac Rocheux	Lac des Sables	Lac Mallard	Lac Rubaniers	Lac François	Lac Boivin	Lac S. Louis	Riv. du Diable	Ruisseau Boivin
G. lugens	83.0*	63.2	64.9	89.7	6.6	61.2	60.9	76.4	14.1	–	73.5	39.6	6.4
G. affinis	14.0	17.6	1.9	0.8	0.6	8.8	6.5	3.2	0.4	–	–	18.9	70.2
G. latilimbus	0.6	11.0	0.3	2.6	–	–	23.0	8.8	87.8	14.3	23.5	35.1	4.6
G. pugionis	–	3.4	0.5	–	–	–	7.3	5.9	–	66.7	–	–	3.2
G. ventralis	–	1.6	–	–	–	–	1.5	–	–	–	–	–	–
G. dichrous	0.6	0.7	–	0.8	–	–	–	–	–	–	–	–	–
G. fraternus	–	0.5	0.8	–	83.8	–	–	–	–	–	–	3.6	–
G. pectoralis	0.6	0.7	22.8	2.6	–	–	0.3	–	–	–	–	0.9	–
G. impressicollis	–	0.3	0.2	–	–	.	–	–	–	–	–	–	–
G. frosti	0.3	0.3	–	–	–	4.7	0.3	5.9	1.6	–	–	–	13.7
G. gehringi	–	0.5	–	–	8.6	–	–	–	–	–	–	–	–
G. instabilis	–	–	8.0	–	0.3	–	–	–	–	2.4	3.0	–	–
G. minutus	–	–	0.5	3.4	–	25.3	–	–	–	–	–	1.8	–
G. bifarius	–	–	–	–	–	–	–	–	–	16.7	–	–	1.8
G. lecontei	–	–	–	–	–	–	–	–	–	–	–	–	–
Nombre d'individus examinés:	329	380	587	116	290	170	261	34	247	42	34	111	220

*Valeurs exprimées en pourcentage.

présence n'a pas été remarquée le long de la rivière du Diable. Capturé de mai à septembre.

Gyrinus affinis Aubé

Ce gyrin corpulent abonde à la plupart des lacs, étangs et mares visités. Toutefois, parmi les populations examinées au lac Monroe, à peine a-t-il été possible de vérifier sa présence. Les eaux stagnantes ont sans doute ses préférences. Observé de mai à septembre.

Gyrinus bifarius Fall

Ce Gyrin semble rare dans la région. En effet, au cours de 1952 et 1953, nous avons répéré six individus seulement parmi les abondantes collections effectuées au lac Monroe. Au cours de 1954, nous l'avons capturé à deux autres endroits de la rivière du Diable, au lac Nansen, ainsi que dans un émissaire commun à plusieurs petits lacs qui déversent leurs eaux dans le lac des Sabes. A ce dernier endroit, plus de 40 individus furent capturés en compagnie de G. gehringi, G. affinis et G. lugens. Observé en mai, juillet, août et septembre.

Gyrinus confinis Lec.

Il ne semble pas faire de doute que cette espèce soit caractéristique des eaux courantes. Nous l'avons observée dans de nombreuses associations obtenues du lac Monroe. Son taux de fréquence toutefois ne dépasse pas généralement deux pour cent. La seule autre récolte de cette espèce dans la région du parc eut lieu au lac Brochet où quatre exemplaires seulement furent rencontrés parmi les quelque 1800 examinés. Observé depuis le milieu de mai jusqu'aux derniers jours d'août.

Gyrinus dichrous Lec.

Cette petite espèce a été capturée dans une dizaine de lacs de la région, mais nulle part elle n'est abondante. Les lacs dystrophes lui conviennent beaucoup moins que les lacs eutrophes. Dans la moitié environ des collections effectuées au lac Monroe, elle était représentée. Observé de mai à septembre.

Gyrinus fraternus Couper.

C'est le Gyrin qui domine dans toutes les associations recueillies au lac Monroe. Il représente environ 60% de toutes les colonies étudiées. Dans les autres types d'habitats, il est extrêmement rare. Sa présence alors s'explique peut-être par des déplacements occasionnels. Observé de mai à septembre.

Gyrinus frosti Fall

Toutes nos collections de Gyrins dans la région n'ont permis de retracer qu'une douzaine d'individus de cette espèce. La plupart furent capturés sur les eaux du lac Monroe. A d'autres lacs, tels le lac des Femmes, le lac Brochet, le lac Nansen, le lac Lauzon, un seul individu fut obtenu. Dans notre province, l'espèce n'avait été citée auparavant que de la région de Hull (Kazabazua, Brown).

Gyrinus gehringi Chamb.

On trouve cette espèce dans de nombreux lacs, mais elle ne forme que rarement des colonies nombreuses. Apparemment, les lacs eutrophes lui conviennent mieux que les lacs dystrophes. Nous n'avons remarqué aucun individu parmi les collections provenant du lac Monroe. Cependant, nous l'avons obtenue de lacs situés au voisinage de la rivière tels que le lac aux Atocas, le lac des Femmes, etc. Observée de mai à septembre. Cette mention serait la première pour notre province et même pour le Canada.

Gyrinus impressicollis Kirby

De taille intermédiaire entre les Dineutes et la plupart des Gyrins, G. *impressicollis* ne manque pas d'attirer l'attention. C'est l'espèce que Fall qualifiait de "almost mythical" et de "extremely rare" et dont il ne connaissait l'existence que de sept individus; un provenant du lac Huron et six capturés le long du chemin de fer qui se rend à la baie d'Hudson. Depuis, Brown l'a signalé de Kazabazua. Dans la région du parc du mont Tremblant, en particulier sur le lac Monroe, elle est décidément commune, des milliers d'individus y vivent en compagnie de *Gyrinus fraternus* principalement. Sur les autres lacs de la région, sa présence n'est qu'occasionnelle. Capturé de mai à septembre.

Gyrinus instabilis Fall

Cette espèce s'est montrée abondante à trois endroits visités; ailleurs, seuls deux ou trois individus furent capturés. Les lacs peu profonds où la couche de sédiments est épaisse lui conviennent surtout. Nous l'avons capturée durant la dernière quinzaine de mai, mais aussi durant le reste de la saison estivale. La série qui a servi à Fall pour la description originale provenait de l'Alaska. Il ne semble pas y avoir eu d'autres citations depuis. Cette découverte de l'espèce dans les Laurentides ajoute donc considérablement à l'aire de distribution connue.

Gyrinus latilimbus Fall

Cette petite espèce fut trouvée dans la plupart des associations étudiées. Cependant, sur les eaux du lac Monroe et du lac Lauzon, elle était beaucoup plus clairesemée qu'à la plupart des autres lacs où des collections furent opérées. Il ne fait pas de doute que les adultes préfèrent tournoyer sur les eaux peu profondes à travers une dense végétation de Carex ou de Scirpes. Observé de mai à septembre.

Gyrinus lecontei Fall

Assez général sur les étangs et mares, ce Gyrin devient moins fréquent sur les lacs proprement dits. La larve s'accommode apparemment d'un habitat qui se dessèche durant quelques semaines en été, du moins, c'est principalement sur les eaux peu profondes qu'on rencontre l'adulte. Il envahit les ruisseaux qui alimentent les lacs ainsi que les émissaires, où parfois il s'attroupe en colonies nombreuses. Observé de mai à septembre.

Gyrinus lugens Lec.

A la plupart des lacs, ce Gyrin est, sinon l'espèce dominante, du moins l'une des plus abondamment représentée. Il s'accommode de tous les types d'habitats: eaux claires ou troubles, vives ou stagnantes. Observé de mai à septembre.

Gyrinus minutus Fab.

Toutes proportions gardées, se petit Gyrin doit être considéré comme rare dans la région étudiée. Nulle part, nous n'avons capturée plus de quelques individus à la fois et, à la plupart des lacs, il a semblé manquer tout à fait. Les lacs tourbeux ou semi-tourbeux ont ses préférences. Observé durant les mois de mai, juin et août.

Gyrinus pectoralis Lec.

Sa distribution est assez limitée, mais, en général, là où il se rencontre, il forme des colonies extrêmement nombreuses. Les lacs encaissés dans les montagnes à la tête d'un bassin de drainage l'attirent plus particulièrement. On rencontre toutefois quelques individus ici et là sur d'autres types de lacs. Capturé de mai à septembre.

Gyrinus pugionis Fall

C'est le Gyrin qui domine aux lacs tourbeux et semi-tourbeux. Il envahit parfois les émissaires de ces lacs, quand il s'en trouve, mais ne s'y aventure qu'à peu de distance. Peut-être fuit-il tout simplement les rayons solaires. Sa présence dans d'autres types de lacs se rattache parfois à un micro-habitat apparenté au type tourbeux. Capturé depuis le milieu de mai jusqu'à la fin d'août.

Gyrinus ventralis Kirby

Dans la plupart des associations étudiées au lac Monroe, nous n'avons obtenu que quelques rares individus de cette espèce. Ailleurs, nous ne l'avons remarquée qu'au lac des Femmes et au lac Nansen. Sa présence dans le parc du mont Tremblant semble très limité. Observé de mai à septembre.

Conclusions

1. L'étude de nombreuses colonies et associations de Gyrinidés prélevées dans une cinquantaine d'étendues lacustres a permis de trouver dans le secteur méridional du parc du mont Tremblant seize espèces de *Gyrinus* et deux espèces de *Dineutus*.

2. Le *Gyrinus instabilis* Fall et le *Gyrinus gehringi* Chamberlain sont apparemment nouveaux pour la faune canadienne. D'autres espèces, telles G. *impressicollis* Kirby, G. *pugionis* Fall, G. *frosti* Fall, qui n'avaient été signalées qu'une seule fois pour notre province (région de Hull, Brown), ont été récoltées à nouveau et parfois en très grande abondance.

3. Un inventaire complet de la population de Gyrins qui habitent une étendue d'eau exige l'étude de récoltes abondantes et nombreuses.

4. Les colonies de Gyrins qui évoluent sur les lacs et les étangs du parc du mont Tremblant sont habituellement formées de plusieurs espèces qui vivent de concert et forment des associations définies. Chaque type d'association, variable selon l'habitat, est dominé par des espèces caractéristiques différentes.

5. L'étude de la composition des associations de Gyrins peut servir d'indice biologique du milieu dans lequel ils vivent.

6. Dans un lac donné, les diverses colonies de Gyrins montrent le plus souvent beaucoup d'homogénéité de composition; cependant, il arrive que certaines colonies soient notablement différentes, indice de micro-habitats variés.

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The Influence of Spray Programs on the Fauna of Apple Orchards in Nova Scotia.   VIII. Natural Enemies of the Eye-Spotted Bud Moth, *Spilonota ocellana* (D. & S.) (Lepidoptera: Olethreutidae)[1]

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The eye-spotted bud moth, *Spilonota ocellana* (D. & S.), has a long history as a pest in Nova Scotia apple orchards, serious damage by it being reported as early as 1891 (Fletcher, 1892). Its status has fluctuated considerably, the most notable outbreak reaching its peak in 1927. This outbreak occurred when dusts were being used for the control of orchard pests, and (Kelsall, 1932) was one of the two main reasons for abandoning the general use of dusts after 1927. The bud moth declined rapidly after 1927 and by 1931 was rated a minor pest (Gilliatt, 1932a). After fluctuating at relatively low levels for seven years, it increased in importance and by 1942 was again a major pest. From 1942 to 1952, there was little change in its general status although large fluctuations in population were observed in orchards in which certain insecticides had been used (Stultz, 1950). During 1953, there was a marked decline in the average population level although reductions did not occur in all orchards.

It has become increasingly apparent that, within the limitations imposed by climatic conditions, population levels of the bud moth vary greatly as a result of interactions between spray chemicals and biological control agents (Gilliatt, 1932b; Mendall, 1941; Stultz, 1951; Pickett and Patterson, 1953).

In this paper, the known biological control agents of the eye-spotted bud moth in Nova Scotia are listed, together with an estimate of their relative importance. Some indication is also given of the extent to which their population densities are influenced by spray programs.

Parasites

The primary parasites of the eye-spotted bud moth in Nova Scotia listed in Table I were, except for one species, found in samples taken in 26 to 70 orchards annually from 1946 to 1953. The orchards, including experimental, commercial, and a few neglected plantings throughout the Annapolis Valley, provided as wide a range of conditions as possible, including different spray treatments.

In sampling for parasites, the various parasite-host relationships were studied at appropriate times during the year. This involved the sampling of bud moth material in hibernacula, "spin-ups", webs on leaves, and eggs on leaves. The kind and amount of parasitism were determined either by rearing adults from samples of the host population or, when possible, through the recognition of immature forms, cocoons, and pupal remnants. Since 1948, the determination of the distribution and abundance of the principal parasites has been based largely on the latter method. Immature forms of the internal parasites were observed by dissection of host larvae; when unknown species were encountered, this method was supplemented by rearing.

The status of *Agathis laticinctus* (Cress.) has changed greatly since 1947, when it was an important biotic control agent only in the comparatively few neglected orchards and in those not sprayed with arsenicals. By 1952, it was observed in all of the 70 orchards sampled, parasitism exceeding 10 per cent in

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TABLE I

Frequency of occurrence of primary parasites of the eye-spotted bud moth in Nova Scotia

Parasite	Frequency*
Hymenoptera: Ichneumonidea	
Braconidae	
Meteorus trachynotus Viereck...............................	Common
Agathis laticinctus (Cresson)................................	Abundant
Apanteles sp. near *acaudus* (Provancher).....................	Rare
Apantales sp., *? sarrothripae* Weed........................	Rare
Apanteles tmetocerae Muesebeck............................	Rare
Ascogaster quadridentata Wesmael..........................	Common
Bracon gelechiae Ashmead................................	Rare
Ichneumonidae	
Scambus alboriecta (Cresson)...............................	Rare
Scambus sp. near *atrocoxalis* (Ashmead)....................	Rare
Scambus hispae (Harris)...................................	Common
Scambus pterophori (Ashmead).............................	Rare
Scambus sp..	Common
Pimpla aquilonia Cresson..................................	Rare
Itoplectis quadricingulatus (Provancher)....................	Rare
Ischnus inquisitorius atricollaris (Walsh)...................	Rare
Campoplex validus (Cresson)...............................	Rare
Campoplex sp..	Rare
Cremastus sp..	Rare
Atrometus clavipes (Davis)................................	Common
Hymenoptera: Chalcidoidea	
Trichogrammatidae	
Trichogramma minutum Riley..............................	Abundant
Eulophidae	
Euderus subopacus (Gahan)...............................	Common
Diptera	
Tachinidae	
Actia diffidens Curran....................................	Rare
Phrynolydella eufitchiae (Townsend).......................	Rare
Mericia sp...	Rare
Nemorilla pyste (Walker).................................	Rare
Phorocera erecta Coquillet................................	Rare

*Abundant, observed in most orchards sampled during recent years, frequently parasitizing over 10 per cent of a population; common, observed in many of the orchards sampled but seldom or never numerous; rare, rarely collected, never numerous.

75 per cent of these orchards and 50 per cent in slightly more than 30 per cent (Stultz, 1954). The maximum parasitism observed was 93 per cent.

Egg parasitism by *Trichogramma minutum* Riley varied and showed little relationship to orchard practices except that the use of DDT or parathion, when bud moth eggs were present, always resulted in little or no parasitism. Reduction of bud moth populations by this parasite apparently depended largely on the population densities it attained on other hosts before bud moth eggs were laid. Parasitism by *T. minitum* was negligible from 1945 to 1948, but in every year since it has been of considerable importance in many orchards, averaging from 12 to 23 per cent but seldom exceeding 40 per cent.

Parasitism by *Scambus* spp. was general but was usually low, seldom exceeding 10 per cent and never exceeding 33 per cent.

Parasitism by *Meteorus trachynotus* Vier. was either absent or so low as to escape observation in two-thirds or more of the orchards sampled each year. It occasionally exceeded 10 per cent, seldom exceeded 20 per cent, and did not exceed 60 per cent.

Parasitism by *Ascogaster quadridentata* Wesm. was similar to that of *M. trachynotus* except that it less often exceeded 20 per cent and did not exceed 38 per cent.

Parasitism by *Euderus subopacus* (Gahan), which attacks second- to fifth-instar larvae, was often very low or absent regardless of the spray program. It seldom exceeded 20 per cent and never exceeded 33 per cent.

The pupal parasite *Atrometus clavipes* (Davis) occurred in very small numbers in most orchards. Parasitism seldom exceeded 1 per cent and did not exceed 10 per cent.

The only parasite listed in Table I that was not observed during the present study was *Apanteles tmetocerae* Muesebeck, which was collected by Brittain (Muesebeck, 1921). Others collected previously in Nova Scotia were: *Agathis laticinctus* (=*Microdus ocellanae* Richardson) and *Ascogaster quadridentata* (misnamed *Chelonus* sp.), reared by Sanders and Dustan (1919); *Nemorilla pyste* (Wlk.) and *Phorocera erecta* Coq., which were reared by Gilliatt in 1927; and *Trichogramma minutum*, collected by Sanders and Dustan (1919) and by Gilliatt (1932b).

Adults collected during this study were identified by officers of the Entomology Division, as follows: Braconidae, Mr. G. S. Walley, Dr. W. R. M. Mason, and Mr. C. D. F. Miller; Ichneumonidae, Mr. G. S. Walley and Dr. W. R. M. Mason; Chalcidoidea, Dr. O. Peck; Vespidae, Mr. G. S. Walley and Mr. C. D. F. Miller; Tachinidae, Mr. G. E. Shewell and Mr. A. R. Brooks.

Predators

The predators listed in Table II were observed feeding on the eye-spotted bud moth in small cages or free in the orchard. *Anystis agilis* Banks and *Deraeocoris nebulosus* (Uhler) fed only on early-instar larvae; the wasp *Ancistrocerus catskill albophaleratus* (Saussure), whose juglike mud cells were often found in the abandoned nests of the eastern tent caterpillar, *Malacosoma americanum* (F.), collected only mature larvae.

Several species of spiders were seen feeding on bud moth adults in small cages, but *Paraphidippus marginatus* (Walckenaer) was the only one identified. This spider also attacked bud moth adults in apple trees.

The arthropod predators varied greatly in numbers. Some were often so scarce as to escape detection by the usual method of sampling, i.e., the jarring method described by Lord (1949) and MacPhee (1953). Another method, more inclusive but more cumbersome, involving the fumigation of whole trees, indicated that all but two of the arthropod predators listed in Table II were usually present in their appropriate seasons on apple trees unless highly toxic spray materials had been applied (MacPhee and Sanford, personal communication). The two exceptions were the unidentified coleopterous larva, which was rarely found, and the wasp *Ancistrocerus catskill albophaleratus*, a wide-ranging hunter. Except the *Atomus* mites and the unidentified Nabidae, the remaining arthropod predators were common, in the sense that they were often collected by the jarring method.

Kelsall (1950) observed the following birds feeding on mature or nearly mature bud moth larvae: the least fly catcher, the song sparrow, the savannah sparrow, the chipping sparrow, the yellow warbler, the blue-headed vireo, and the redstart. The writer observed members of a flock of white-winged crossbills opening "spin-ups" to feed on bud moth larvae.

TABLE II.

Feeding proclivities* of predators of the eye-spotted bud moth as indicated by the use of small cages and field observations.

Predator	Predacious on	
	eggs	larvae
Arachnida		
Aranae		
Agelenopsis sp.	–	++
Coriarachne versicolor Keyserling	–	++,T
Dictyna sp.	–	+
Misumena calycina (L.)	–	++,T
Paraphidippus marginatus (Walckenaer)	o	++,T
Tmarus angulatus (Walckenaer)	–	++
Acari		
Anystis agilis Banks	+	++,T
Atomus sp.	++	
Insecta		
Neuroptera		
Undetermined chrysopid larvae	o	++
Thysanoptera		
Haplothrips faurei Hood	++,T	o
Leptothrips mali (Fitch)	++	o
Hemiptera		
Pentatomidae		
Podisus modestus (Dallas)	o	++,T
Euschistus tristigmus (Say)	–	++
Nabidae		
Undetermined species	–	+
Anthocoridae		
Anthocoris musculus (Say)	+	++
Miridae		
Hyaliodes harti Knight	++	+
Deraeocoris fasciolus Knight	+	+
Deraeocoris nebulosus (Uhler)	o	++
Coleoptera		
Undetermined larva	–	++,T
Coccinellidae		
Adalia bipunctata (L.)	–	++
Anatis 15-punctata var. *mali* (Say)	–	+
Coccinella transversoguttata Faldermann	–	++
Coccinella perplexa Mulsant	–	+
Hymenoptera		
Vespidae		
Ancistrocerus catskill albophaleratus (Saussure)		T
Birds (See Kelsall, 1950)		

*No information; ++, fed readily in cages; +, fed sparingly in cages; O, failed to feed in cages; T, seen feeding free on trees in orchard.

Little progress has been made in determining the relative importance of the predators in the field, largely because of the exceedingly short period of close association between a predator and its prey.

Among egg predators, *Haplothrips faurei* Hood ranked highest because it frequently attained high population densities, generally causing high egg mortality.

None of the predators on bud moth larvae can be stated as being definitely more important than any of the others. As a rule, the predators left little or no evidence of their work other than missing bud moth larvae. Even the few dead larvae with indications of predation could not be related to the predator causing their deaths except those killed by chrysopid larvae and these seldom appeared in field collections. Evidence of predation by the wasp *Ancistrocerus catskill albophaleratus* was detected only by examining their mud cells.

Disease

The only disease found definitely associated with bud moth mortality was a polyhedral virus. Dr. F. T. Bird, Insect Pathology Laboratory, Sault Ste. Marie, Ontario, who examined diseased bud moth larvae collected from apple trees in Nova Scotia, stated (personal communication) that the polyhedral bodies "resemble very much those found in the spruce budworm". So far, the disease has been recognized only in late-instar larvae collected during June and early July. Dead larvae are at first somewhat swollen, show extreme liquefaction, and burst open very readily when handled. Later they collapse and dry to form a shapeless smear. The incidence of diseased larvae varied greatly from year to year and from orchard to orchard. Though the virus was occasionally of considerable importance, it seldom destroyed over 10 per cent of a population.

Effects of Spray Chemicals on Beneficial Arthropods

The available information on the effects of spray chemicals on bud moth parasites is summarized in Table III; similar data on predators were reported by MacPhee and Sanford (1954).

TABLE III.
Effects* of spray chemicals on the principal parasites of *S. ocellana* in Nova Scotia

Parasite / Chemical	Glyodin	Ferbam	Copper	Sulphur	Nicotine sulphate	Parathion	DDT	Arsenical	Cryolite
M. trachynotus	O	+O	O	+O	−	−	++	++	−
A. laticinctus	O	O	O	O	O	O	O	++	−
A. quadridentata	O	+O	O	+O	−	−	++	++	−
Scambus spp.	O	O	O	O	−	++	++	+	O
A. clavipes	O	O	O	O	−	−	O	O	−
T. minutum	O	O	O	+O	O	++	++	O	O
E. subopacus	O	O	O	O	+O	−	++	++	+O

*No information; O, no apparent reduction of numbers; +, reduction; ++, practical elimination; +O, possible reduction, evidence inconclusive.

The records for parasites and predators indicate that the use of DDT or parathion is followed by a drastic reduction in numbers of predators and of the more important parasites except *Agathis laticinctus*. There is considerable evidence that parasitism by the latter is favourably influenced by the use of DDT (Stultz, 1950; Stultz, 1954).

The regular use of arsenicals was followed by little or no reduction in numbers of predators except *Anystis agilis* but drastically reduced those of the more important parasites except *Trichogramma minutum*. Nicotine sulphate caused a reduction of several predators. Its use for the control of the rosy apple aphid, *Anuraphis roseus* Baker, in the spring and of the bud moth in mid July apparently did not reduce the numbers of the parasite *T. minutum* or *Agathis laticinctus*.

Sulphur and dichlone were the only fungicides that seriously reduced the numbers of any of the bud moth predators; both were detrimental to *Haplothrips faurei* and sulphur reduced the populations of *Leptothrips mali* (Fitch), *Anystis agilis*, and *Anthocoris musculus* (Say).

All the principal parasites were observed at relatively high levels after a copper or glyodin fungicide was used.

Meteorus trachynotus and *Ascogaster quadridentata* were only rarely seen after several years' use of either ferbam or flotation sulphur, so that it is possible their numbers were reduced, to some extent, by these fungicides.

Agathis laticinctus attained relatively high levels of parasitism in experimental orchards where glyodin, ferbam, copper, or sulphur was used without insecticides over a period of several years. For example, in 1949, after four years of spraying with copper, ferbam, or flotation sulphur, the observed parasitism by *A. laticinctus* was 36, 26, and 47 per cent respectively. Sulphur was then replaced with glyodin. In 1952, after seven years of spraying with copper or ferbam or three with glyodin, the observed percentages of parasitism were 43, 60 and 65 respectively.

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Moisture and Diapause in the Wheat Stem Sawfly, *Cephus cinctus* Nort. (Hymenoptera: Cephidae)[1]

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Introduction

Dryness of either an insect's habitat or its food has often been reported as inducing diapause. This has been well substantiated in *Pectinophora* (8, 21, 22) and *Loxostege* (23). Also, a difference in body moisture between forms of the same species, in diapause and not in diapause, has been recorded in *Leptinotarsa* (9), *Lucilia* (11), and *Carpocapsa* (24), there being less water in the insects in diapause. It is significant, though, that in preparing for diapause *Leptinotarsa* achieves a reduction in moisture content, even when there is an abundance of water outside, by excretion (4).

Further, it has been demonstrated in *Leptinotarsa* (5, 9), *Pyrausta* (3), *Epiblema* (16), *Lucilia* (11), *Diprion* (14), *Melanoplus* (20), *Carpocapsa* (24), and *Locustana* (10) that the water lacking during diapause must be replaced before post-diapause development can proceed. Squire (21) found that supplying contact water to *Pectinophora* expedited its emergence from dormancy or facilitated its subsequent development, but that it was not essential. From such information has arisen the idea, often casually repeated, that an external moisture supply is necessary for diapause development. But, as Andrewartha (2) emphasized, data presented by most of the authors just mentioned have indicated that the provision of water is necessary only after hibernation. None showed water to be critical during diapause development. The water deficit must be remedied before post-diapause development can take place, but an external water supply has not been proved to have much influence on diapause development itself. Readio (15) found that *Reduvius* completed diapause even more successfully at low humidities. Similarly Matthée (10) specified that in *Locustana* diapause development is best promoted by a dry environment, though moisture is required at its completion.

An apparent contradiction to the idea that contact moisture is probably unnecessary for diapause development is found in the work of Slifer (20), who showed that diapause in *Melanoplus differentialis* (Thos.) eggs could be broken by treating them with xylol and other fat solvents. These presumably dissolved a waxy coat and permitted the entry of water into the egg, thereby breaking diapause. However, Andrewartha (2) suggested that xylol may have eliminated diapause by way of other, direct effects on the egg contents. Andrewartha's suggestion is supported by the fact that xylol can break diapause in *Myrmus* eggs, which contain enough moisture when laid to carry them through to hatching (25). Pepper (13), too, found xylol and other chemicals effective in breaking diapause in *Loxostege* prepupae, in which impermeability to water is probably not a factor.

Against this background of evidence, diapause in the wheat stem sawfly, *Cephus cinctus* Nort., was investigated in its relation to moisture conditions.

In *C. cinctus* the mature S-shaped larva enters a fall diapause soon after it has cut off the ripe wheat stem above the short stub in which it overwinters. By early spring, diapause development is invariably completed and post-diapause development can begin. Salt (19) found that diapause development proceeds most rapidly at 10°C. At this temperature two to four months is required to bring most specimens through diapause. It proceeds much more slowly at 15° and 5°C., and if a larva has received some conditioning at 10°C. it can often complete its diapause development even as low as 0°C., and rarely as high as 20°C.

Under natural growing conditions diapause is firmly established in every mature S-larva at the end of the crop season. Perhaps dryness plays a part in establishing it, but no larva ever escapes diapause; hence an investigation into the effect of dryness in this connection is impractical. But the extent to which diapause development, or diapause breaking, depends on moisture is pertinent.

Also significant is moisture's role in diapause reinstatement in *C. cinctus*, an event apparently unique among insects.

Ainslie (1) observed that *C. cinctus* larvae in the field sometimes failed to develop in the spring though they were obviously viable. He attributed this to insufficient moisture. There now is little doubt that the larvae had been returned to diapause early in the spring. In extensive areas of Alberta and Saskatchewan a severe early drought in 1937 killed the sawflies' host plants and nearly annihilated the progeny of that year. In spite of this there was a sawfly outbreak in 1938. Large numbers of the previous brood must have returned to diapause in the spring of 1937, and emerged in the spring of 1938 to cause the unexpected plague (7). In 1944 a similar carry-over occurred. In some infested fields in eastern Alberta, 85 per cent of the stubs still contained undeveloped S-larvae after the flight was over. Many of the larvae survived and in the spring of 1945 they emerged as normal adults about the same time as others of the next generation. Another observation of this kind was reported by Mills, Callenbach, and Reinhardt (12), who wrote that undeveloped S-larvae were found in 50 per cent of a stand of infested stubs on July 18, 1944.

This "spring diapause" occurs frequently in small portions of populations whose microhabitats are especially hot and dry (7).

Salt (19) confirmed that diapause, though once broken, could be reintroduced by the action of heat. Exposure to 35°C. for 25 days during the larva's transition from diapause development to post-diapause morphogenesis caused all larvae to revert to diapause. On the Great Plains heat and drought are usually closely associated, so that the possibility presented itself that dryness, too, might influence the reinstatement of diapause. Since dryness prompts the original

entry into diapause in some species, it was doubly possible that it could reinduce dormancy in *C. cinctus*. In the present investigation of dryness and diapause, of course, the proved importance of temperature could not be disregarded and experiments were performed at a variety of temperatures.

Only one intimation of a possible similar reinstatement of diapause in insects was found in the literature. Prebble (14) observed that a dry spring prevented the development of *Diprion*, which undergoes a prepupal diapause; in a bivoltine race development commenced if water was supplied later during the summer, but members of a univoltine race did not so respond, possibly having gone back into diapause. Faber (5) reported that in *Leptinotarsa* an individual occasionally has two diapauses, one as a very young adult and the second the next year after the reproductive period, but this seems to be very different from the situation in *C. cinctus*.

Materials and Methods

The mature sawfly larvae used in this work were collected from wheat fields near Lethbridge, Alta. Roots and debris were removed from the infested wheat stubs, which were then packed loosely in moist garden soil in closed pint jars for storage.

Most experiments reported here required S-larvae that were ready to begin post-diapause development but had not yet begun it. In some of these, spring-collected post-diapause material was used, but generally it was not reliably uniform, part of it having already developed too far. For this reason much of the stock was gathered in the fall while still dormant. Diapause was broken in the laboratory under strictly controlled conditions to obtain the desired material. Since diapause development progresses most rapidly at 10°C., this temperature was used for the first part of the larvae's conditioning. But because morphogenesis will also take place, at least to some extent, at 10°C. the stubs were removed to 0°C. as soon as the first few larvae had emerged from dormancy. Several months' storage at 0°C. broke diapause in the remainder and permitted them to finish most of the development occurring between diapause and post-diapause morphogenesis. None of them could begin post-diapause morphogenesis at 0°C. In this way a stock was prepared of fairly uniform post-diapause S-larvae, ready to recommence morphogenesis as soon as they were incubated.

A supply of larvae in diapause for use in several experiments was maintained by storing fall-collected stubs in slightly moistened soil at 25°C., a temperature too high to permit any diapause breaking. This temperature and the 10° and 0°C. temperatures mentioned above were maintained in constant temperature rooms with an accuracy of ±0.5°C.

Two experiments dealt with moisture absorption during and after diapause development; others concerned the effects of dryness and heat on diapause reinstatement. In each case larvae were treated and incubated while intact in their stubs because the initiation of development after dormancy is very easily prevented if they are removed.

After a post-diapause S-larva has begun metamorphosis and transformed into a prepupa, or even a day or so before this, it will continue to develop under most conditions until it either becomes adult or dies. At moderate temperatures, and if excessive drying is prevented, it develops normally and at about the same speed, whether in or out of the stub. Removal from the stub at this time has little effect. Just before this, however, during the period between the end of diapause and shortly before the larva becomes a prepupa, removal from its stub very frequently checks further progress, even when temperature, moisture, and

light conditions are apparently favourable. The insect remains active and healthy for months but will not develop. This inhibition will affect a variable and often a large portion of any sample of larvae in this stage. Moreover, the only criterion available for determining the presence or absence of diapause in a C. cinctus larva is whether it will change form when incubated. All attempts to measure the influence of dryness on diapause reinstatement using naked larvae were futile; they had to be kept in their stubs.

In experiments where humidity was controlled it was done over sulphuric acid solutions or dry calcium chloride in glass desiccators. High temperature exposures (over 25°C.) were made in cabinets in which temperature fluctuations were less than ±1°C.

Whenever the number of larvae capable of development was to be determined, or conversely, the number still in or returned to diapause, samples of stubs were covered with moist soil in closed pint or half-pint jars and incubated at 25°C. The employment of moist soil for post-treatment incubation was an important feature of the experimental procedure. The main objective of this work was to measure the influence of dryness in producing a true and enduring diapause. Of less concern was the extent to which it would cause a temporary arrest of development whereby development would soon begin again if the insect's water deficit was eliminated. By incubating treated specimens with an abundance of moisture, temporary effects of dryness would be nullified and only the lasting effects recorded. The minimum incubation period was three weeks, which was long enough to permit larvae to become adult if they began development promptly. Wherever a treatment tended to delay the initiation of morphogenesis, incubation was extended as much as three weeks longer.

The moist soil in which larvae were treated or incubated was sandy loam containing about 15 per cent moisture. The dry soil used in some experiments was similar soil, air-dried at room temperature.

Moisture contents were determined on individual larvae. They were removed from the stub, weighed on a spring-torsion balance (150/0.1 mg.), oven-dried, and reweighed. Drying for one day at 95-100°C. was sufficient to bring the specimens to constant weight.

Normal Moisture Absorption During and After Diapause

The water present in a sawfly larva's tissues during dormancy is normally supplemented by absorption of soil moisture before pupation. This was demonstrated by the following experiment. S-larvae in diapause obtained from a moist field on September 1, 1953, were kept in moist soil at 10°C. to continue their diapause development. After 0, 30, 60, and 90 days at 10°C. samples of more than 70 larvae were tested for water content, and other samples in two replicates, each sample containing about 30 larvae, were incubated at 25°C. to determine the number in which diapause was terminated. Young prepupae developing from S-larvae given 120 days at 10°C. plus seven days' incubation, and more advanced prepupae (11 days' incubation), were also tested for water content. As a check a moisture content determination was also made on larvae in diapause stored 150 days in moist soil at 25°C. The results are shown in Table I. Some water was taken up during diapause development, and even more just before and during prepupal morphogenesis. In addition there was a loss of dry matter by the insects that approached in quantity the water absorbed. These two processes combined to produce the increase in moisture: dry weight ratios as development progressed. Salt (18) has already shown that C. cinctus larvae can absorb contact water, and it was evident in this experiment that water

TABLE I

Water absorption in *C. cinctus* larvae during and after diapause and during prepupal development, as indicated by ratio of water to dry matter

Number of days at 10° C.	Percentage of larvae out of diapause	Average ratio of water to dry matter
0........................	0	0.97 ± 0.01
30........................	0	1.14 ± 0.02
60........................	43	1.20 ± 0.02
90........................	80	1.25 ± 0.01
120........................	99	—
Young prepupae		1.34 ± 0.02
Advanced prepupae		1.65 ± 0.02
S-larvae in diapause, stored 150 days at 25°C. in moist soil		1.10 ± 0.01

absorption contributed more to the change in the moisture: dry matter ratios than did catabolism. Note that the controls stored at 25°C. absorbed little moisture. Water uptake must be regulated according to the insect's stage of development and is not merely a passive process.

Additional sawflies from the same source as those above were enclosed in jars of dry soil for 30, 60, 90, and 120 days at 10°C. and then incubated in moist soil. The percentage of each sample that developed upon incubation, and therefore the portion in which diapause must have been eliminated, is compared with that of larvae chilled in moist soil (Table II). It is clear that there were no differences. In the dry series there was no possibility of water absorption; probably a little dehydration occurred. Evidently diapause development is not dependent upon absorption of external moisture, and can proceed normally without it, provided, of course, that excessive dehydration has been prevented.

Other sawfly larvae were kept in dry soil at 10°C. for 120 days and then incubated in dry soil, thereby receiving no moisture at any time. In two such samples only 26 and 36 per cent developed. In the insects in which development

TABLE II

Diapause elimination in *C. cinctus* larvae at 10°C., with and without access to moisture

Number of days at 10°C.	Percentage developing when incubated moist after chilling at 10°C. in	
	dry soil	moist soil
30........................	0	0
60........................	36	43
90........................	83	80
120........................	100	99

ultimately did occur it began several days late. Water absorbed near the end of diapause must be essential for many members of a sawfly population if they are to undergo metamorphosis, though to some it is not a critical factor. But a moisture supply during dormancy is not a requisite. That diapause development in the wheat stem sawfly is independent of an external moisture supply offers additional support to Andrewartha's (2) suggestion that this situation is general among insects.

Another experimental series similar to each of the various groups described above, but composed of larvae obtained in 1952, gave very nearly the same results. The weight of water absorbed, however, exceeded the reduction in dry material by a greater margin in this series. Also, it showed more clearly that some of the water absorbed is taken up during the transition period between diapause development and post-diapause morphogenesis. This transition can be accomplished at either a moderate (25°C.) or low (10°C.) temperature; development during this interval is not dependent on low temperature as diapause development is, yet no substantial physical changes take place until it is finished. The transition period is arbitrarily considered as terminating about a week before the S-larva transforms visibly into a prepupa if the insects are reared at 25°C. in the laboratory, or at the beginning of warm spring weather if they are in the field.

The second series also clearly showed that additional water was not needed during diapause development.

Effect of Dryness on Diapause Reinstatement and Initiation of Morphogenesis

Although contact water was unnecessary for elimination of diapause in *C. cinctus*, there still remained the possibility that lack of moisture or dehydration could re-establish diapause. It has already been pointed out that dryness brings about diapause in several insect species. However, the two situations are dissimilar. The question being considered is whether *C. cinctus* larvae are influenced by dryness just after a long period of relative inactivity, and long after feeding has ceased. The other species are influenced during their growing and feeding stages, becoming dormant only after some delay, no doubt after devious and intricate body processes.

If we assume for the moment that dryness does help to establish a second diapause, it may act under one or more of a variety of conditions: (a) it may act independently of the influence of temperature extremes, i.e., during incubation at 25°C.; (b) it may supplement the action of heat in reinstating diapause if heat and dryness are combined in one treatment; (c) a decreased body water content, previously produced by dehydration at a subdevelopmental temperature, may cause a larva to return to diapause upon incubation; or (d) a decreased water content produced as in (c) may facilitate the action of high temperature in returning the larva to diapause. These four possibilities will be considered in turn.

a. *Influence of Dryness During Incubation*

The first possibility was easily eliminated. It was soon realized that in post-diapause larvae incubated at 25°C. lack of moisture was not a potent enough factor to prevent morphogenesis. Larvae incubated from the beginning of their transition stage in a current of dry air developed past the critical period for diapause reinstatement before enough drying was achieved. Even when 1952 material, which had a long transition period—one that lasted two weeks at 25°C.—, was subjected to this treatment practically all larvae developed. As a group the larvae lost only 9.6 per cent of their original water before the critical period was past. The average ratio of water to dry matter was reduced from 1.36 to 1.26.

b. *Influence of Dryness when Combined with Heat*

In a number of different experiments post-diapause larvae in their stubs were subjected to drying and heat simultaneously for less than a day or for several days. At 50°C. nearly all of them died within 12 hr., and at 45°C. within two days. Desiccation produced some mortality, but heat alone was the more important factor although at the end of the most severe treatments the insects were completely dried up. Most of those that endured sublethal treatments failed to develop when subsequently incubated at 25°C. in moist soil. However, there was no indication that desiccation contributed to the inhibition of development; about as many survivors ceased developing whether they had been heated moist or dry. Larvae inhibited from developing by the action of temperatures of 45°C. or more are now believed to be crippled rather than in diapause. This point will be discussed more fully in another paper.

Larvae survived at least a week at 40°C. and very much longer at 35°. A week at 35°C. usually caused all of them to revert to diapause, and here again it seemed to matter little whether they were moist or dry during treatment. These experiments suggested that diapause is less quickly reinstated at 40°C. than at 35°. After treatment at 40°C., if an insect did not die, it was more likely to develop than if it were treated at 35°C.; and of those whose development was blocked at 40°, some no doubt were permanently injured by the heat. Again, at 40°C. dryness was ineffective in arresting development.

In another trial the behaviour of post-diapause larvae was compared at 35°C. while their stubs were lightly covered with moist soil and with dry soil. Those treated in the dry soil were subject to some dehydration, under much the same conditions that they might experience during a spring drought. Duplicate samples of 40 stubs were treated for 2, 4, 6, and 8 days and then were incubated for development, moist at 25°C. The percentages of insects in which diapause was reinstated are given in Table III. There was no mortality. The results of the two series, moist and dry, are so closely parallel that it is certain that lack of moisture was immaterial.

c. *Effect of Desiccation at 0°C.*

The experiments described so far showed contact moisture to be of little importance in the initiation of post-diapause morphogenesis and diapause rein-

TABLE III

Diapause reinstatement in post-diapause *C. cinctus* larvae by heating at 35° C. in moist and dry soil

Duration of treatment, days	Percentage returned to diapause	
	moist	dry
2	28	19
	20	19
4	83	82
	76	88
6	97	95
	100	100
8	100	100
	100	100

statement at temperatures suitable for incubation or higher. They also showed that desiccation did not contribute to re-establishment of diapause at those temperatures. However, the larvae used had already had access to moisture before the attempts at diapause reinstatement. It is important to know what would happen if similar larvae were dehydrated at a subdevelopmental temperature before they were incubated or exposed to heat. By such treatment, water that had been absorbed during diapause could be eliminated before any development could begin. This procedure was tried in two experiments. In these, conditions were equivalent to late winter desiccation in the field, whereas previous experiments had simulated desiccation during the first heat of spring.

For the first experiment infested stubs were gathered in the fall and diapause was eliminated at 10° and 0°C. They were then dehydrated by a dry air current at 0°C. for 0, 30, and 60 days. During the first 30 days the larvae lost 9 per cent of their original moisture; in 60 days, 24 per cent. The average ratio of water to dry matter was 1.51 before treatment, 1.30 after 30 days, and 1.16 after 60 days of desiccation. Moderately severe desiccation was achieved. After desiccation the larvae were incubated in moist soil. The numbers that failed to

TABLE IV

Inhibition of post-diapause morphogenesis in *C. cinctus* by dehydration at 0°C.

Treatment	Number surviving	Number not developing	Percentage not developing
Desiccated 0 days...................	85	3	4
Desiccated 30 days.................	82	5	6
Desiccated 60 days.................	73	23	32
No desiccation; 120 days at 0°C., moist	57	6	11

develop are listed in Table IV. The more severe desiccation prevented morphogenesis in nearly one-third of them. In a control sample kept twice as long at 0°C., but in damp soil, most larvae developed. Thus most of the effect must be attributed to dryness and not to storage at 0°C.

In the other experiment, stubs from three sources were dehydrated for 5, 20, and 50 days at 0°C. and 0 per cent relative humidity. The pretreatment histories of the three groups of stubs were: (a) Collected in the field in the fall and stored nearly 20 months at 0°C. after diapause was broken, the latter part of this interval being spent in dry soil (upon incubation some would not develop). (b) Collected in the fall, and stored at 0°C. to break diapause but not permitted to become dry. (c) Collected in early spring (April 10) (these were slightly ahead of (b) in development). A sample of 70 stubs from each combination of treatment and pretreatment was then incubated for three weeks at 25°C. in moist soil to permit recovery of lost water. Another was incubated without soil in a covered jar to permit neither absorption of moisture nor further desiccation.

The results (Table V) show that two factors determined whether larvae developed promptly when incubated, developed after some delay, or did not develop at all. They were the persistent effect of desiccation at 0°C., and

TABLE V

Development of post-diapause *C. cinctus* larvae after desiccation at 0° C.

Pre-treatment	Days desiccated at 0° C.	Incubated	Number of				Percentage not developing
			S-larvae	prepupae	pupae	adults	
(a) Collected in fall; diapause broken; stored at 0° C. in moist, then dry, soil.	5	dry	38	7	2	1	79
	20	dry	38	4	2	0	86
	50	dry	30	0	0	0	100
	5	moist	15	0	4	24	35
	20	moist	19	3	8	8	50
	50	moist	25	1	3	2	81
(b) Collected in fall; diapause broken; kept moist.	5	dry	2	2	2	56	3
	20	dry	1	0	4	37	2
	50	dry	9	4	2	27	21
	5	moist	0	0	0	65	0
	20	moist	1	0	2	56	2
	50	moist	2	1	0	50	4
(c) Collected in early spring; kept moist.	5	dry	0	2	4	26	0
	20	dry	1	0	1	32	3
	50	dry	1	4	4	27	3
	5	moist	0	0	2	31	0
	20	moist	0	0	2	21	0
	50	moist	0	1	0	29	0

dryness during incubation at 25°C. Sawflies collected in early spring (c) had advanced far enough and had absorbed enough water to be practically unaffected by moderate amounts of desiccation. When incubated moist, development was uninhibited. In a few insects, however, dryness during incubation did delay the beginning of development. In fall-collected material (b), besides delaying development somewhat, dry incubation preceded by 50 days' dehydration at 0°C. prevented development in some specimens. Desiccation at 0°C. followed by moist incubation failed to prevent development in any significant portion of the larvae. In fall-collected larvae, moderate desiccation with subsequent incubation in moist soil was very effective in blocking development only if the larvae had already been subjected to dryness during their pretreatment (a).

Still longer desiccating exposures would have given more pronounced results. However, the exposures employed were already more severe than any that one would expect to occur naturally.

From this experiment one would infer that a long dry period at subdevelopmental temperatures sometimes causes *C. cinctus* larvae to reenter diapause. But the criterion used up to this point to indicate the presence of diapause, i.e., failure to develop when incubated, is not adequate by itself. Non-developing larvae, if they are actually in diapause, should regain activity if they are chilled, and chilling has proved ineffective in reactivating larvae with a developmental block introduced by dryness.

If post-diapause development has been blocked by heating at 35°C. the block can be removed by chilling. At various times a second diapause was produced in five groups of larvae from different sources, by heating, moist, at 35°C. for one to two weeks. When incubated for several weeks they did not develop. But they did develop after chilling at 10°C. for two to four months

or at 5°C. for a longer time. Thus the developmental block instituted by heat is a real diapause. On the other hand chilling at 10°C. for as much as five or six months failed to remove the barrier in four sets of larvae that were dried and then failed to develop when supplied with moisture again. Probably the inhibition of development caused by dryness is a pathological condition from which the larvae cannot recover, and is not truly diapause.

d. *Influence of Reduced Body Moisture on Reinstatement of Diapause by Heat*

In the following experiment larvae that had been desiccated at 0°C. were given various exposures to 35°C. to test the effect on diapause reinstatement by heat of a moisture content previously established at a low level. One series of post-diapause larvae was dried 60 days at 0°C. in a dry air current. A second series of the same stock meanwhile was kept moist at 0°C. Then two groups of 50 stubs from each series were subjected to 0, 2, 4, and 6 days at 35°C. and 95 per cent relative humidity in attempts to reestablish diapause. Treatment was followed by moist incubation at 25°C. Table VI shows that in about 16 per cent of the insects development was precluded by the desiccation alone, even in the absence of any exposure to 35°C. However, comparison of the results of equivalent heat exposure on desiccated and non-desiccated larvae reveals that, when desiccated larvae received a heat treatmnt, their having been dried did nothing to promote diapause reinstatement. Rather, previous dehydration hindered the diapause-reinstating action of heat. An adjusted chi-square analysis showed the differences between the two series, with the exception of the two-day exposures, to be significant at the one per cent level. The experiment supports the conclusion reached in the preceding section that moisture deficiency and heat prevent development in very different ways.

In a repetition of this experiment the water loss during the 60-day dehydration was measured. The average ratio of water to dry material was reduced from 1.93 to 1.24, a substantial reduction. As a group the insects lost 36 per cent of their original body water. This trial gave results very much like the first.

Discussion

Reference has already been made to the fact that insects of some species enter diapause if they have been kept dry or have fed on dry food. Possibly this is

TABLE VI

Influence of moisture content of post-diapause *C. cinctus* larvae on reinstatement of diapause by heat

Time at 35° C. days	Not desiccated		Desiccated 60 days	
	Number of insects surviving	Percentage not developing	Number of insects surviving	Percentage not developing
0.	42	0	38	18
0.	44	0	37	14
2.	37	49	40	45
2.	36	53	37	32
4.	43	91	39	69
4.	40	83	41	63
6.	45	100	43	86
6.	39	100	36	94

true of *C. cinctus* also, that it is the dryness of the ripening wheat stalk, perhaps in conjunction with other things, that commits the sawfly to its fall diapause. From this it does not necessarily follow that moisture, or a scarcity of it, will continue to be a decisive factor during the insect's passage through the diapause stage. In the wheat stem sawfly it is not an important factor and it probably is not important in other insect species either, so long as little actual desiccation is permitted. After diapause is over the situation changes, however. Then, in some species, including most wheat stem sawfly specimens, the insect must have access to a certain amount of moisture or it will develop no further.

Of the species in which dryness has been shown to produce diapause, nearly all live on plants that regularly ripen and dry at the end of the growing season. This gradual drying up of the host plant is generally a signal worth heeding. Many insects have evolved means of taking advantage of the signal, and enter diapause in response to it, thereby better protecting themselves from the harsher weather to follow. Insects similarly respond to other signals,—e.g., low or declining temperature, short photoperiod and change in food supply—that enable their diapauses to become synchronized with the seasons. This behaviour is good evidence that diapause is not solely an undesirable delay in the life-cycle arising from an unhealthy condition, as it is commonly considered to be.

The tendency towards diapause has probably been selected in the evolution of many insects because of its survival value. Other characteristics have been selected as well, for their value in resisting the same adverse conditions. For example, insects store extra food in their bodies for nourishment during the interval when feeding is impossible. The reduced water content so often found in insects in diapause may also be a protective device, or it may be a secondary adaptation of the insect to the dormant state. The presence of a low water content would naturally be associated with the occurrence of diapause if they both favoured survival. Their frequent occurrence together is not proof that one causes the other.

Again, in the return of *C. cinctus* to diapause moisture conditions are inconsequential. As would reasonably be expected, one can dry a grub so much that it receives permanent injury and on that account does not develop, but one can not recall diapause by dehydration. In fact, the only measured effect of drying was in the opposite direction, though it was a rather small one.

The implications of this study are reassuring from the standpoint of forecasting and controlling wheat stem sawfly infestations. The important effects of winter and early spring moisture conditions are the direct action of dryness in killing the insects by desiccation, and the effect of moisture on soil temperature; there appears to be no reason to include a third category, the influence of moisture on alteration of the life-cycle. A recommended control measure is shallow spring cultivation to bring the stubs to the surface, where the developing prepupae and pupae may dry out and die (6). If this is done before the S-larvae have begun metamorphosis, however, there is the danger that the exposed stubs may be warmed enough, and early enough, that larvae inside will revert to diapause. The relatively resistant S-larval form (17) will persist and may well survive another year. Very early drying of the stubs, so long as they are not heated as well, presents no such hazard; this can only harm the larvae, if not by killing them, then by interfering with diapause re-establishment, though the latter may not actually be important.

In predicting the extent to which spring diapause and the two-year life-cycle might occur, an estimate should be possible on the basis of soil temperature, time,

and, of course, the stage of the insect. There is probably not much to gain by the added consideration of the moisture supply. At 95°F. diapause reinstatement can take place in two days to a week. The temperature of the soil just beneath the surface should only have to exceed 92° or 93°F. for a few days during the latter part of April or the first week or two of May (in Western Canada) in order to affect at least some of the sawfly population.

The antagonism demonstrated between heat and subnormal moisture content in diapause reinstatement is of further interest. In combination with other observations it suggests that a *C. cinctus* larva must reach a certain stage of post-diapause development before it is able to revert to diapause. The requirement may be a specific point in the chain of hormone secretion that activates morphogenesis and pupation. Exposure to 35°C. seems to stimulate this endocrine activity and cause it to advance to some extent, before the heat reintroduces diapause. It has been observed that dryness and desiccation retard the initiation of post-diapause development. Perhaps they operate by inhibiting hormone production or release. A partly dried insect would reach the stage where diapause may again intervene more slowly than one with a normal moisture content. To return a dehydrated insect to dormancy, then, heat would first have to overcome the inhibitory action of dryness and stimulate the endocrine mechanism into activity. Then its "destructive" action could begin.

Summary

Cephus cinctus larvae normally absorb contact water during diapause and prepupal development; moisture thus absorbed is unnecessary for diapause development but in many specimens it is required for the initiation of post-diapause morphogenesis.

The influence of dryness in returning post-diapause larvae to dormancy was investigated. The driest conditions attainable at 25°C. did not prevent development of healthy larvae in their stubs. At higher temperatures dryness was also ineffective, or its influence was obscured by the stronger action of heat. Moreover, previous dehydration at subdevelopmental temperatures did not enhance the diapause-reinstating activity of heat. On the other hand, prolonged desiccation at a low temperature often did prevent larvae from developing any further, even though they were subsequently moistened and warmed. In other larvae development was merely delayed until a favourable water balance could be restored.

When a larva's development was arrested by desiccation it could not be resumed. Such larvae did not respond to chilling as do larvae in diapause. Therefore the desiccation must permanently injure them and the developmental block introduced by dryness is not a true diapause.

Acknowledgments

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Systellogaster ovivora Gahan (Hymenoptera: Pteromalidae) Reared from Egg Capsules of the Wood-roach, *Parcoblatta pennsylvanica* (DeGeer), Collected at Rondeau Park, Ontario

By W. W. JUDD

On September 21, 1953 the writer collected several egg capsules of the wood-roach, *Parcoblatta pennsylvanica* (DeGeer), from beneath the bark of dead, fallen trees in Rondeau Park, Kent County, Ontario. The capsules were put in a jar for rearing. During December 7 and 8, 1953 eight chalcidoid wasps, two males and six females, emerged from the capsules. They were identified as *Systellogaster ovivora* Gahan (family Pteromalidae) by Dr. O. Peck, Systematic Entomology, Department of Agriculture, Ottawa, who pointed out that this was the first Canadian record of this genus. One male and three females from this collection are deposited in the Canadian National Collection.

A second collection of egg capsules of *P. pennsylvanica* was made in Rondeau Park on September 11, 1954 from beneath the bark of fallen trees. Some of the capsules were widely isolated from one another beneath the bark along the length of a log but the majority were found in definite clusters of some two or three dozen in a restricted area of a few square inches beneath the bark. About two hundred capsules were found. Most of them were empty, the nymphal roaches having emerged, leaving the capsules open along their dorsal seams. Two dozen intact capsules were kept for rearing, each being put in a separate shell vial of dimensions 60 mm. x 15 mm., plugged with cotton. On October 5, 1954 one capsule yielded 24 nymphs of *Parcoblatta pennsylvanica*. Another capsule yielded 14 adult *Systellogaster ovivora*: 2 ♂ ♂, 4 ♀ ♀ on October 12, 2 ♀ ♀ on October 13, 3 ♀ ♀ on October 14, 2 ♀ ♀ on October 15 and 1 ♀ on October 17, 1954. The capsule from which the wasps emerged was slightly over 1 cm. long (Fig. 1) and the wasps emerged through two holes, one 1 mm. and the other 0.7 mm. in diameter, chewed in the wall of the capsule. Edmunds (1953) reports that in emerging these wasps sometimes make two or three openings at different places on the same capsule.

Systellogaster ovivora was described by Gahan (1917) from specimens reared from egg capsules of *Blatta orientalis* collected in Illinois. Gahan also refers to specimens reared from egg capsules of a "Blattid" in Maryland. Thompson (1950) and Peck (1951) list *S. ovivora* as a parasite of *Blatta orientalis*. Edmunds
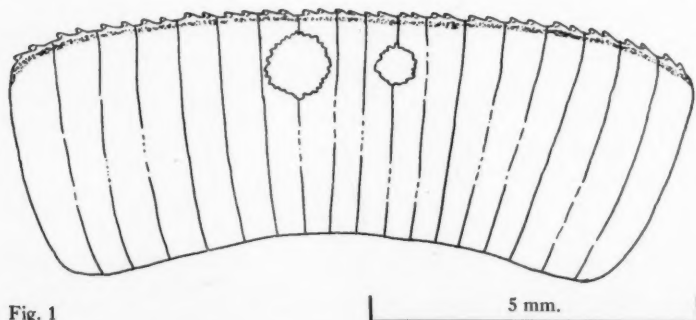

Fig. 1   5 mm.

Egg capsule of *Parcoblatta pennsylvanica* perforated by emergence holes of *Systellogaster ovivora*.

(1952, 1953) made collections of egg capsules, mostly of *Parcoblatta pennsyl-vanica*, in Ohio.   The majority of the capsules were found under the loose bark of fallen trees.   From these he reared several species of wasps, including *Systello-gaster ovivora*.   One of his collections, consisting of twelve capsules, yielded 328 specimens of *S. ovivora* (Edmunds, 1953) giving an average yield per capsule considerably greater than the yield of 14 specimens from the one capsule collected at Rondeau Park.   All specimens reared from the capsules gathered at Rondeau Park are in the collection of the University of Western Ontario except the four deposited in the Canadian National Collection.

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Book Review

THE LEPIDOPTERA OF NOVA SCOTIA, Part 1, Macrolepidoptera, by D. C. Ferguson, Nova Scotia Museum of Science, Halifax, 214 pp.   16 pls., 7 figs.   Proceedings of the Nova Scotian Institute of Science, 23, Part 3. 1954.   Price $2.00.

This excellent publication is essentially an illustrated catalogue of 68 species of butterflies and approximately 760 species of moths known to occur in Nova Scotia.   All known data on distribution, food plants, habitat, habits, flight period, and abundance are included.   Type localities and references to original descrip-tions or subsequent publications of species described from Nova Scotia are given. The specific name is followed by any known common name.   Two hundred and seven species and the main habitat types are illustrated.

The introductory part consists of a historical review of studies on the lepi-dopterous fauna of Nova Scotia since the appearance of the first paper dealing with this subject, published in 1864.   Interesting discussions on the geography, climate, geology, and botany as they affect the Lepidoptera of Nova Scotia are included.   The various Nova Scotia habitats are described and examples of indigenous species are given for each.   Notes are also included on collecting methods.

The book was carefully prepared and reflects the experience and the tireless collecting of the author.   It will remain a valuable reference to all students of Lepidoptera for many years.

A short bibliography and an index of the species and genera are appended.

T. N. FREEMAN

The Systematic Relationships of Dichaetoneura Johns. and Phytomyptera Rond.

By W. R. THOMPSON
Commonwealth Institute of Biological Control

In *The Canadian Entomologist* for January 1953 (pp. 19-30) the writer described the larval forms of *Dichaetoneura leucoptera* Johns. and discussed the relationship of the genus Dichaetoneura which was regarded by Johnson (1907) as closely related to Phytomyptera Rond. and later reduced to a synonym of this genus by Curran (1934). He pointed out that there are rather marked differences between the two genera in adult characters and expressed a doubt that Dichaetoneura could be classed with the Actiines as in the Manual of Myiology of Townsend (Manual of Myiology, IV.). He further remarked on the similarity between the adults of Phytomyptera and Schizactia noting briefly some of the larval characters of Schizotachina and Schizactia which are quite different from those of Dichaetoneura. In a later paper on *Hyalomyodes triangulifera* Loew (*Can. Ent.*, Vol. LXXXVI, No. 3) he gave data on the larval forms of Schizotachina, Schizactia and Psalidopteryx.

Unfortunately no information was available in regard to the larval stages of Phytomyptera. This has now been provided in a valuable paper by Dr. Egidio Mellini, published in the "Bollettino dell' Istituto di Entomologia dell' Universita di Bologna" (Vol. xx, 1954, pp. 309-332). Mellini's figures and descriptions show that the first, second and third stage mouth hooks are extremely similar to those of Schizotachina. The anterior spiracles of the mature larva possess 11-14 papillae arranged in a ring, while Schizotachina has 15-17. The posterior extremity terminates in a very distinct tail, and in this unusual feature Phytomyptera also agrees with Schizotachina and Schizactia. Even the cuticular spines appear to be of the same form.

The work of Mellini thus confirms the writer's view that Phytomyptera is not closely related to Dichaetoneura but is rightly placed with the Actiines.

Supplements to *The Canadian Entomologist*

It is exrtemely difficult at the present time, to find an avenue of publication for long scientific papers. The editors of periodicals published in parts of 25 to 50 pages, like *The Canadian Entomologist*, find that the diversity of the interests of its readers must be recognized by the provision of a variety of articles dealing with many different aspects of the special science covered by the journal. Long papers occupying the whole or the greater part of a number can rarely be accepted, yet only in such papers can certain subjects be adequately dealt with.

The publishers of *The Canadian Entomologist* have therefore decided, as opportunity offers and financial support is available, to issue supplements devoted to long monographs or comprehensive treatises. The first supplement, devoted to the internal anatomy of sawfly larvae, will appear shortly and will be distributed free to subscribers and members of the Entomological Society of Canada. We believe that the readers of *The Canadian Entomologist* will approve this venture.   W. R. THOMPSON

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Larval colony of *Pristiphora erichsonii* (Htg.) feeding on larch foliage, *Larix laricina* (Du Roi) K. Koch. (Photograph by D. C. Anderson, Sault Ste. Marie).